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INHERITANCE OF CROSS- AND SELF-STERILITY AND SELF-FERTILITY IN BETA VULGARIS [1]

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INTRODUCTION

Difficulty in securing self-fertilized seed from cultivated varieties of *Beta vulgaris* L. has been commonly experienced. Self-fertility, which contrasts strikingly with the more common self-sterile condition, is now becoming familiar to most breeders of sugar beets and garden beets. Various self-sterile types and a limited number of self-fertile types of sugar beets were collected by the writer, with emphasis upon selections from curly top resistant varieties. Genetic studies of cross-sterility, self-sterility, and self-fertility were conducted upon selected parental material having clearly defined differences, careful account being taken of variability caused by environmental factors.

REVIEW OF LITERATURE AND THEORY

Papers dealing with sterility in *Beta vulgaris* have been written by Archimovitch (*1*),[3] Brewbaker (*3*), Briem (*4*), Down and Lavis (*8*), Hallqvist (*15*), Kohls (*20*), Magruder (*23*), Munerati (*24*), Raleigh (*26*), Stewart (*28*), and Sundelin (*30*). Self-fertile types of beets have been described by Archimovitch (*1*), Kharechko-Savitskaĭa,[4] Magruder (*23*), Stewart, Lavis, and Coons (*27*), and Sundelin (*30*). The basis of inheritance of self-sterility and self-fertility in *Beta vulgaris* has apparently received but little attention.

It will be seen that instances of sterility behavior in *Beta vulgaris* obtained by the writer are somewhat complex but are fairly well explained by certain modifications of the oppositional hypothesis (*10*, *13*). The oppositional hypothesis supposes the presence in the style of substances that produce incompatibility when a pollen tube enters with an *S* factor in common with stylar tissue. An S^1S^2 plant is sterile or incompatible with all its own S^1 and S^2 pollen, and with S^1 and S^2 pollen from any other source, but fertile with S^3 to S^n pollen, S^1 to S^n representing an allelic series. Crosses of the type $S^1S^2 \times S^3S^4$ yield four classes, $S^1S^3+S^1S^4+S^2S^3+S^2S^4$. Cross-sterility in both

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[3] Italic numbers in parentheses refer to Literature Cited, p. 697.

[4] KHARECHKO-SAVITSKAĬA, E. I. [KHARETCHKO-SAVITZKY, E.] AUTOSTERILITÉ ET AUTOFERTILITÉ CHEZ LA BETA VULGARIS L. Inst. Internatl. de Rech. Betteravières Assemblée, Compt. Rend. Définitif 4: 127-129. 1934. [Processed.]

directions between all plants within any one of these four classes is expected, but crosses between different classes should be fertile. A cross of the type $S^1S^2 \times S^2S^3$ produces two classes, $S^1S^3 + S^2S^3$, one of which is identical with the pollen parent.

The factor S^f for self-fertility (*9*, *12*), allelic to the sterility factors S^1 to S^n, is exceptional and does not produce self-sterility. Heterozygous S^fS^a plants upon selfing are expected to produce only self-fertile offspring (S^fS^f and S^fS^a) without recovery of the S^aS^a genotype because of sterility to S^a pollen.

With a single series of oppositional factors, self-sterile plants are normally heterozygous for S factors. Consequently, if a cross is fertile in one direction, it is expected to be fertile in the other direction. Nonreciprocal behavior is expected only after the unusual selfing of self-sterile plants. Selfing a self-sterile plant, S^1S^2, may yield three classes, $S^1S^1 + 2\ S^1S^2 + S^2S^2$, with nonreciprocal sterility between the first and second and between the third and second classes.

Although nonreciprocal cross-sterility is not commonly expected with a single series of oppositional factors, Lawrence (*21*) has shown that nonreciprocal behavior may commonly result with duplicate oppositional factors, a condition expected with polyploidy. This theory seems to fit certain results to be described with beets, although there is little reason to expect polyploidy with the $2n=18$ chromosome condition (*2*) in *Beta vulgaris*. Lawrence's theory of duplicate factors assumes that duplicate or identical genes are carried by two different chromosomes. The duplicate of S^1 will be designated Z^1, the genes being identical but carried by different chromosomes. Confusion because of failure to consider S^1 and Z^1 identical has been experienced (*22*, *29*). It is assumed that a single S or Z factor carried by the pollen and not present in stigmatic tissue produces fertility, hence an $S^1S^1Z^1Z^2$ female should be fertile with S^1Z^3 or S^3Z^2 pollen. The behavior of the duplicate factors will be illustrated further as results are interpreted.

EXPERIMENTAL PROCEDURE

MATERIAL

One of the early curly top resistant strains produced by Carsner (*6*) and known as 12c proved to be of interest because of a strong degree of cross-sterility. After preliminary studies from closely bred material within the 12c strain, three plants, designated clones 1, 2, and 4, were selected in 1931 for intensive studies. Self-fertility arose from selfing the self-sterile clone 4, presumably by mutation. Another of the original curly top resistant strains, known as 286 (*6*), segregated for self-fertility, and strain 1167, selected from strain 286 in 1931, was found to carry the genetic factor S^f for self-fertility. Carsner (*6*) had done considerable inbreeding in developing the 286 strain from which 1167 was derived, and the 12c strain was also obtained by relatively close breeding Self-sterile plants were found to predominate greatly in the curly top resistant variety U. S. 1 (*7*), and a few individuals whose degree of self-sterility was known from extensive experience were propagated vegetatively for genetic investigations.

Some of the extensive selections made by Tracy,[5] without regard to curly top resistance, were tested for self-sterility and self-fertility.

[5] William Woodbridge Tracy, Jr. (1872–1932), formerly associate agronomist, Bureau of Plant Industry, U. S. Department of Agriculture, was stationed at Fort Collins, Colo., from 1915 to 1928, in connection with sugar-beet investigations.

Some of these selections were rather strongly self-sterile, but the Tracy strain 2769 was found to segregate for self-fertility, and a selection, designated clone 70, was propagated vegetatively and utilized for genetic studies.

METHODS

It was recognized at the beginning of the work in 1930 that a study of self-sterility and self-fertility in beets would require vegetative propagation to carry critical material along for perhaps several years. Fortunately, the task of building vegetative clones was not difficult, because succulent cuttings from vegetative seedstalks took root readily and clones were easily carried along from year to year with a moderate degree of attention. The most critical factor was the matter of inducing seedstalks to become vegetative, to insure vigorous cuttings. This was accomplished by controlling light and temperature in a manner described by Owen, Carsner and Stout (*25*).

Paper bags made of several kinds of material were used in testing compatibility. The most suitable were those made from ordinary 30-pound parchment butter wrappers, 8½ × 11 inches. These wrappers were folded and glued by hand; then a strip of varnish was painted over the seams to prevent moisture from interfering with the glue. Lightweight kraft bags of various sizes also proved useful, but for steri'ity studies there is considerable advantage in having a white and partly translucent bag so that the pollen can be readily seen. A large bag is usually not necessary to detect sterility relationships. To determine self-fertility or self-sterility of the blossoms, the paper bags were placed on the branches prior to flowering. Crosses were made by exchanging paper bags at the proper time, and with self-sterile plants as female parents there was no need for emasculation.

It was useful to know that beet pollen can be stored at low temperatures. Kharechko-Savitskaĭa (*18*) reports germination from beet pollen stored for 49 days at low temperature and low humidity. The writer stored pollen for various periods in an electric refrigerator at approximately 36° F. and found some viable pollen even after 60 days. A week's storage has been considered entirely safe and was adopted whenever it was impossible to have plants flowering at the same time.

The bagging work was first done in the open field, but it soon became apparent that there were many advantages in using the greenhouse. Here insect and weather damage were largely eliminated, and by adjusting day length and temperature it was possible to keep plants in flower over a longer period.

RESULTS

HERITABLE AND ENVIRONMENTAL INFLUENCES COMPARED

Both environmental and heritable influences were observed to affect self-sterility in beets. An example of a heritable difference in degree of self-sterility is as follows: During the spring of 1932, branches from two vegetative clones selected from the U. S. 1 variety were bagged at flowering time. Clone 36, with 17 paper bags, did not produce a single seed, while clone 73 produced a total of 15 seeds in 17 bags (11 of the 17 bags produced no viable seeds). Further observation indicated that the difference between these two clones was consistent.

Other examples of differences in degree of self-sterility could be cited from experience with other vegetative clones. There appeared to be gradations up to occasional intermediate types that were sometimes difficult to distinguish from truly self-fertile types. Nevertheless, the truly self-fertile condition was clearly defined and was seldom confused with the common self-sterile condition that predominates in commercial varieties of sugar beets.

In the field, types with a self-sterile tendency, single-plant or single-clone isolations set seed more easily than parts of the same plants under paper bags. Evidently the paper bags interfered with fertilization to some extent, or with the development of the embryo. Clone 4 of the 12c strain and clone 86 of the Pioneer variety of sugar beets furnished examples of practically complete self-sterility in field isolations as well as under paper bags. With each of these clones a very small amount of the seed produced in favorable field isolations turned out to be chiefly red garden beet hybrids. Since no red beet or Swiss chard plants were observed to be flowering in the vicinity of the isolations, this contamination probably resulted from distant sources of pollen. Contamination was probably encouraged by the high degree of self-incompatibility, which caused the flowers to remain unfertilized and the stigmas receptive for a relatively long period. In other instances clones that were classed as self-sterile from tests with paper bags produced fairly good seed in field isolations. The best field results with self-fertilization were secured in the higher valleys of northern Utah (5,000 to 6,000 feet elevation), where temperatures were lower than in Salt Lake Valley (about 4,300 feet elevation).

A surprising amount of self-fertilized seed was set on some self-sterile plants in early summer near the end of each season's work in the greenhouse and after a prolonged period of flowering. Experience with clone 19, a selection from the 12c strain, was particularly conspicuous. For 2 years this clone was studied in connection with cross-sterility with other 12c plants. Results were confusing the first year (1931), but near the end of the next spring this clone produced self-fertilized seed in abundance in the greenhouse. A month earlier the same plants were strongly self-sterile, and a further test of new plants of the same clone in the field in 1932 again indicated complete self-sterility. A similar observation was made with the self-sterile clone 144 derived from the U. S. 1 variety. A quantity of self-fertilized seed was secured late in the season on an old plant after the clone had been studied for a period of 4 years and always observed to be strongly self-sterile. It was apparent after these experiences that classifications for self-fertility were not always reliable on old plants late in the season in the greenhouse, after a prolonged period of flowering.

It is perhaps significant that this unusual self-fertility was most noticeable at the end of the season in the greenhouse on plants that had passed through several flowering periods. The best flowers were usually produced with the first flowering, and under field conditions this is normally the final flowering. In the greenhouse, on the other hand, it is possible to cut off part of the inflorescence and, with proper growing conditions, produce new flowering branches. This process was sometimes repeated four or five times in a season, and self-fertility was most noticeable during the later periods. This resembles

the exceptional self-fertility at the end of the season that East and Park (*11*) have described in self-sterile species of *Nicotiana*. An explanation of this end-season fertility suggested by East and Park (*11*) is the disappearance from the style of substances that had previously been responsible for a chemical antagonism between the stylar tissue and pollen tubes.

NONRECIPROCAL CROSS-STERILITY IN THE 12C STRAIN

A special feature of the cross-sterility found in the 12c strain was a decided nonreciprocal behavior. Many of the observed results, including the nonreciprocal behavior, agree rather well with expected results, assuming duplicate oppositional factors (*21*) for sterility. This theory, therefore, will be described as data are presented, although experiments were not carried far enough to check certain crucial points.

Twenty plants from a closely bred selection from the 12c strain were grown in 1931, and an attempt was made to cross each plant in both directions with the other 19 plants. Three of the 20 plants were inclined to be sterile as females but fertile as pollen parents. Plant No. 4, later designated clone 4, was sterile to pollen from 16 of the 19 other plants, but when used as a pollen parent it was fertile in most combinations. Three plants, clones 1, 2, and 4, were selected for further study. The center of interest was the nonreciprocal cross-sterility among these 3 plants (fig. 1). Clone 4 was sterile to pollen from clones 1 and 2, but clones 1 and 2 were fertile to pollen from clone 4. Clone 2 was sterile to pollen from clone 1, but clone 1 was fertile to pollen from clone 2. These results were clearly defined and were confirmed by means of repeated tests during the course of 4 years' work.

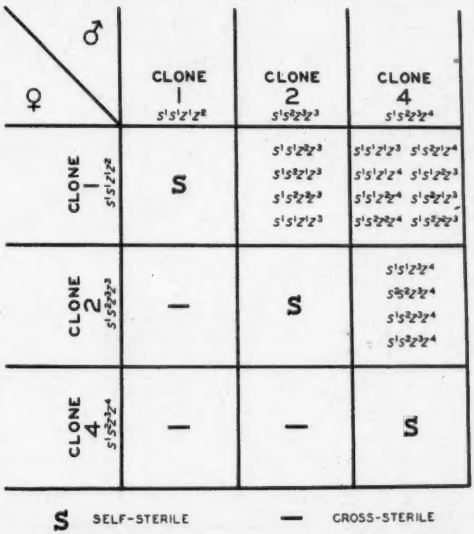

FIGURE 1.—Explanation, on basis of duplicate factors, of nonreciprocal cross-sterility among clones 1, 2, and 4. Genotypes of parental clones shown in margins, and genotypes of all F_1 offspring shown for the three fertile combinations.

To explain the breeding behavior of clones 1, 2, and 4 on the basis of duplicate factors for sterility, good agreement between theory and most of the observations results if it is assumed that clone 1 was of constitution $S^1S^1Z^1Z^2$; clone 2, $S^1S^2Z^3Z^3$; and clone 4, $S^1S^2Z^3Z^4$. The

Z factors are assumed to be exact duplicates of the S factors but carried by different chromosomes; that is, S^1 is assumed to have exactly the same effect as Z^1, and S^2 the same as Z^2, etc. Pollen is assumed to be effective if it carries an allelomorph of either S or Z not present in stigmatic tissue. In accordance with this theory all possible F_1 genotypes for the three fertile combinations among clones 1, 2, and

♀ \ ♂		CLONES			F_1 PLANTS (CLONE 1 × CLONE 2)						
		$S^1S^1Z^1Z^2$ 1	$S^1S^2Z^2Z^3$ 2	$S^1S^2Z^2Z^4$ 4	$S^1S^1Z^2Z^3$ A	— B	$S^1S^2Z^1Z^3$ C	— D	$S^1S^2Z^2Z^3$ E	F	$S^1S^1Z^1Z^3$ G
CLONES	$S^1S^2Z^2Z^4$ $S^1S^2Z^2Z^3$ $S^1S^1Z^1Z^2$										
	1	S	+	+	+	+	+	+	+	+	+
	2	—	S	+	—	—	—	—	—	—	—
	4	—	—	S	—	—	—	—	—	—	—
F_1 PLANTS (CLONE 1 × CLONE 2)	$S^1S^1Z^2Z^3$ — $S^1S^2Z^1Z^3$ — $S^1S^2Z^2Z^3$										
	A	—	—	+	S	—	—	—	—	—	—
	B	—	—	+	—	S	—	—	—	s	—
	C	—	—	+	—	—	S	—	—	—	—
	D	—	—	+	—	—	—	S	—	—	s
	E	—	—	+	—	—	—	—	S	—	s
	$S^1S^1Z^1Z^3$ F	+	+	+	+	+	+	+	+	S	s
	G	+	+	+	F	+	+	+	F	s	S

OBSERVED AND EXPECTED

\+ FERTILE

— STERILE

S SELF-STERILE

EXPECTED BUT NO OBSERVATION

F FERTILE

S STERILE

FIGURE 2.—Observed results and explanation, on basis of duplicate factors, of cross-sterility among F_1 plants from clone 1 × clone 2 and with parental clones 1, 2, and 4.

4 are indicated in figure 1. For the F_1 population derived from clone 2 × clone 4, the genotype $S^1S^2Z^2Z^4$ occurs twice because it is formed in two different ways.

The reactions of the F_1 plants from clone 1 × clone 2 are shown in figure 2. Both theory and observation indicate 2 distinct classes of F_1 plants. According to the theory, 3 genotypes, $S^1S^1Z^2Z^3$, $S^1S^2Z^1Z^3$, and $S^1S^2Z^2Z^3$, carry 3 kinds of genes (S^1 or Z^1, S^2 or Z^2, and S^3 or Z^3)

and are expected to be sterile to pollen from clones 1 and 2 and all of the F_1 plants. Another class of plants, consisting of 1 genotype, $S^1S^1Z^1Z^3$, carries only 2 kinds of genes, and, failing to carry S^2 or Z^2, it is expected to be fertile with half of the pollen from clones 1 and 2 as well as with three-fourths of the pollen from clone 4 and all F_1 plants except those within its own class. The theory requires a 3 : 1

♀ \ ♂	CLONES			F_1 PLANTS (CLONE 2 × CLONE 4)									
	$S^1S^1Z^1Z^2$ 1	$S^1S^2Z^2Z^3$ 2	$S^3S^4Z^2Z^4$ 4	A $S^1S^2Z^2Z^4$	B $S^1S^4Z^2Z^4$	C $S^2S^3Z^2Z^4$	D $S^3S^4Z^2Z^4$	E	F	G	H $S^4S^2Z^2Z^4$	I	J
CLONES 1 $S^1S^1Z^1Z^2$	S	+	+	F	+	F	+	+	+	+	+	+	+
CLONES 2 $S^1S^2Z^2Z^3$	—	S	+	F	F	+	+	+	F	+	+	+	+
CLONES 4 $S^3S^4Z^2Z^4$	—	—	S	—	—	—	—	—	—	—	—	—	—
F_1 PLANTS (CLONE 2 × CLONE 4) A $S^1S^2Z^2Z^4$	F	F	+	S	S	F	F	F	F	F	F	F	F
F_1 PLANTS (CLONE 2 × CLONE 4) B $S^1S^4Z^2Z^4$	F	F	+	S	S	F	F	F	F	+	+	+	F
F_1 PLANTS (CLONE 2 × CLONE 4) C $S^2S^3Z^2Z^4$	F	+	+	F	F	S	S	F	F	F	F	F	+
F_1 PLANTS (CLONE 2 × CLONE 4) D $S^3S^4Z^2Z^4$	+	+	+	F	F	S	S	F	+	+	+	F	+
F_1 PLANTS (CLONE 2 × CLONE 4) E	—	—	—	S	S	S	S	S	S	S	S	S	S
F_1 PLANTS (CLONE 2 × CLONE 4) F	—	—	—	—	S	S	—	S	S	—	—	—	—
F_1 PLANTS (CLONE 2 × CLONE 4) G	—	—	—	S	—	—	—	S	—	S	—	—	—
F_1 PLANTS (CLONE 2 × CLONE 4) H $S^4S^2Z^2Z^4$	—	—	—	S	—	S	—	S	—	—	S	—	—
F_1 PLANTS (CLONE 2 × CLONE 4) I	—	—	—	S	—	S	—	S	—	—	—	S	—
F_1 PLANTS (CLONE 2 × CLONE 4) J	—	—	—	S	S	—	—	S	—	—	—	—	S

OBSERVED AND EXPECTED

\+ FERTILE
— STERILE
S SELF-STERILE

EXPECTED BUT NO OBSERVATION

F FERTILE
S STERILE

FIGURE 3.—Observed results and explanation, on basis of duplicate factors, of cross-sterility among F_1 plants from clone 2 × clone 4 and with the parental clones 1, 2, and 4.

ratio for these 2 classes of plants, while 5 plants (A to E) were observed in the first class and 2 plants (F and G) were observed in the second class. Unfortunately, this theory, which agrees so well with observed results, was not in mind when the sterility reactions were being tested, and critical data regarding sterility between plants F and G (fig. 2) were not recorded. The F_1 plants, clone 1 × clone 2, were also segregated for male sterility. Of 60 plants observed, 40 produced normal

pollen and 20 produced partly or completely aborted pollen. Only plants that produced normal pollen were used in the studies indicated in figure 2.

All observed results agree perfectly with the expected sterility and fertility reactions from the F_1 plants, clone 2 × clone 4 (fig. 3), but several gaps occur in the observations. Half of the F_1 plants, or the

♀ \ ♂		CLONES			F_1 PLANTS (CLONE 1 × CLONE 4)									
		1	2	4	A	B	C	D	E	F	G	H	I	J
CLONES	1	S	+	+	+	+	+	+	+	+	+	+	+	+
	2	−	S	+	+		+		+	+		+	+	+
	4	−	−	S	−	−	−	−	−	−	−	−	−	−
F_1 PLANTS (CLONE 1 × CLONE 4)	A	+	+	+	S	+		+	+			+	+	+
	B	+		+	+	S	+		+	+		+	+	+
	C	+		+	+	+	S		+	+	+		+	
	D		+	+	+			S	+	+				+
	E	−		+	+	+	+		S	+		+	+	+
	F	−	+	+	+	+	+		−	S		+	+	+
	G	−		+	+				−		S		+	+
	H	−		+	+	+		+	+	+		S		+
	I	−	−	−	−	−	−	−	−	−	−		S	
	J	−		−	−				−				−	S

\+ FERTILE
− STERILE
S SELF-STERILE

FIGURE 4.—Observed results of cross-sterility among F_1 plants of clone 1 × clone 4 and with parental clones 1, 2, and 4.

genotypes $S^1S^1Z^3Z^4$ and $S^2S^2Z^3Z^4$, are expected to be fertile as females in all combinations, except in crosses between identical genotypes, and half ($S^1S^2Z^3Z^4$), formed in two different ways (fig. 1), are expected to be sterile as females in all combinations. Figure 3 shows four plants (A to D) that appear to belong in the first class and six plants (E to J) that appear to belong in the second class.

Reactions with clone 4 and F_1 plants, clone 2 × clone 4, were tested further with additional plants grown in the field. An abundance of

pollen, collected in paper bags from 45 F_1 plants, was mixed and applied to branches of clone 4 previously protected from foreign pollen by paper bags. The results were all negative, indicating complete cross-sterility of clone 4 with pollen from all of the 45 plants in the F_1 population. Pollen from clone 4 was also applied to the 45 F_1 plants, and results may be added to those for the 10 plants indicated in figure 3. This makes a total of 55 F_1 plants tested, of which 29 were fertile and 26 were sterile to the pollen from clone 4. This is a good 1:1 ratio and agrees with expected results.

Some of the observed results (fig. 4) with the F_1 plants, clone 1 $\times$ clone 4, do not agree with what is expected from the theoretical considerations. The eight classes of F_1 genotypes ($S^1S^1Z^1Z^3$, $S^1S^1Z^1Z^4$, $S^1S^1Z^2Z^4$, $S^1S^2Z^2Z^4$, $S^1S^2Z^1Z^4$, $S^1S^1Z^2Z^3$, $S^1S^2Z^1Z^3$, and $S^1S\,Z^2Z^3$) expected from clone 1 $\times$ clone 4 are indicated in figure 1. The genes Z^3 and Z^4 do not occur together in any one of these eight genotypes, hence all F_1 plants should be fertile to pollen from clone 4 ($S^1S^2Z^3Z^4$). Observed results with the F_1 plants I and J (fig. 4), which show sterility to clone 4 pollen, are, therefore, not in agreement with the expected results. It can be shown that the theory does not explain the behavior of the F_1 plant I (fig. 4), which was tested in seven of the nine possible combinations with other F_1 plants and was sterile as a female in all combinations for which it was tested. Another disagreement with expected results is the consistently positive reaction of clone 2 with pollen from F_1 plants when a 1:1 ratio of positive to negative reactions is expected.

Other observed results with the F_1 population, clone 1 $\times$ clone 4, are in agreement with the theory of duplicate factors under consideration. The reactions with plant F as a female (fig. 4) are particularly indicative of what is expected. If this plant were of constitution $S^1S^1Z^2Z^4$, $S^1S^2Z^2Z^4$, or $S^1S^2Z^1Z^4$, the absence of the Z^3 gene would explain the negative reaction to pollen from clone 1 ($S^1S^1Z^1Z^2$) and the positive reaction to pollen from both clone 2 ($S^1S^2Z^3Z^3$) and clone 4 ($S^1S^2Z^3Z^4$). If plants A to D (fig. 4) were of constitution $S^1S^1Z^1Z^3$ or $S^1S^1Z^1Z^4$, their consistently positive reactions as females with pollen from clones 1, 2, and 4 and with most of the F_1 plants could be explained.

The experiments were not carried far enough to constitute a critical check on the theory of duplicate factors, but in general the agreement between theoretical and observed results is sufficiently close to warrant careful consideration of this theory in any future work that might be attempted. Reactions among the three parental clones 1, 2, and 4, and results with F_1 plants, clone 1 $\times$ clone 2, and clone 2 $\times$ clone 4, agree remarkably well with expected results on the basis of duplicate factors for cross-sterility. The possibility of modifying genes responsible for lack of agreement between observed and expected results with the F_1 plants, clone 1 $\times$ clone 4, may be considered, but data are too limited to postulate the precise behavior of such modifiers.

INHERITANCE OF SELF-FERTILITY

It will be shown that self-fertility in beets may be determined by a single genetic factor designated S'. Although the inheritance of self-fertility is well explained by this single factor, the allelomorphs of S', expected to determine cross-sterility reactions, could not be identified. The evidence clearly indicates the presence of auxiliary factors for

cross-sterility in addition to allelomorphs of the factor S^f. The exact nature of these auxiliary factors is unknown, but one series of backcrosses gave results in agreement with expectation, assuming a duplicate series of Z factors in addition to the S series. In another series of backcrosses the results failed to agree entirely with expectation based upon duplicate factors.

The designation for homozygous self-fertile plants will be S^fS^f, and for heterozygous self-fertile plants S^fS^a (or S^fS^b or S^fS^x). For convenience all self-sterile plants are arbitrarily designated S^aS^b, although in a group of self-sterile plants many different S allelomorphs may be involved. In general, crosses between self-sterile plants and heterozygous self-fertile plants will be designated $S^aS^b \times S^fS^x$. Here S^x in relation to S^a and S^b is unknown but, without proof to the contrary, it may be assumed in each case to be different from S^a or S^b. When necessary to consider duplicate factors for cross-sterility, different S and Z factors are distinguished by numerical superscripts, with $S^1S^2Z^3Z^4$, etc., representing self-sterile plants and $S^fS^2Z^3Z^4$, etc., representing heterozygous self-fertile plants with the factor for self-fertility limited to the S series. The allelomorph S^f, responsible for self-fertility, is the only factor in the S series whose identity is believed to be established; hence, all other designations are purely arbitrary.

In hybrids to be described, the factor S^f for self-fertility came either from the curly top resistant strain 1167 or from clone 70, a selection from the Tracy strain 2769. The self-sterile clones 90 and 144, used in backcross studies, were derived from the curly top resistant variety U. S. 1.

TABLE 1.—*Backcross and F_2 data for the factor S^f for self-fertility*

Hybrid	Population No.	Self-fertile plants	Self-sterile plants
		Number	*Number*
Self-sterile × heterozygous self-fertile, $S^aS^b \times S^fS^a$:			
08–1 × 01a–1 [1]	[2] 1166	[2] 49	[2] 44
Clone 91 × 2222–150	4382	12	13
Clone 113 × 2222–150	4480	6	4
Clone 139 × 4356A–668	5212	11	10
Clone 139 × 4356A–671	5213	34	37
Clone 139 × 4356A–673	5214	27	30
Clone 139 × 4712–676	5237	7	7
Clone 137 × 5170	6159	38	29
5563–1 and 3 × 5214	6283	22	13
Total		206	187
Heterozygous self-fertile, S^fS^a (or S^fS^b) selfed:			
4356A–1 selfed	5369	7	0
4356A–668 selfed	5373	40	0
4356A–673 selfed	5375	17	0
4514–635 selfed	5426	23	0
4514–643 selfed	5428	10	0
Total		97	0
Self-sterile × homozygous self-fertile, $S^aS^b \times S^fS^f$:			
Clone 4 × 2255–206	3139	108	2
Clone 90 × 2255–7	4356A	7	0
Clone 97 × 2255–7	4407	15	0
3474–35 × 2255–7	4712	16	0
Total		146	2

[1] The population obtained by the self-fertilization of 01a–1 became known as 1167.
[2] Data from population 1166 supplied by F. A. Abegg, Division of Sugar Plant Investigations, Bureau of Plant Industry.

The combined results of crosses between self-steriles S^aS^b and heterozygous self-fertiles S^fS^z used as pollen parents (table 1) show 206 self-fertile and 187 self-sterile plants, which is a fairly good 1 : 1 ratio. This 1 : 1 ratio is in accord with the hypothesis of a single factor for self-fertility.

Selfing heterozygous self-fertile plants S^fS^a (or S^fS^b) produced a total of 97 self-fertile plants (table 1) but no self-sterile plants. This indicates that pollen with allelomorphs S^a or S^b was unable to produce self-fertilization on S^fS^a (or S^fS^b) plants.

Homozygous S^fS^f plants were demonstrated in population 2255. Four populations resulting from self-sterile seed parents $S^aS^b \times$ homozygous 2255, S^fS^f, plants are shown in table 1. All the offspring were expected to be self-fertile, and from 148 plants tested 146 were observed to be self-fertile and 2 self-sterile. The 2 self-steriles may have come from the scant self-fertilization of the self-sterile seed parents, which were not emasculated in making the crosses.

TABLE 2.—*Backcross data for S^f and R*

Population No.	*R* S^f plants	*R* S^x plants	*r* S^f plants	*r* S^x plants
	Number	*Number*	*Number*	*Number*
588	8	8	10	10
590	4	7	6	7
5212	4	7	4	6
5213	17	17	26	24
5214	12	15	15	15
6159	21	17	14	15
6283	14	8	6	7
Total	80	79	81	84
Expected with *R* and S^f independent	81	81	81	81

TABLE 3.—*F_2 data for S^f and R from R r S^fS^x plants selfed*

Population No.	Individuals			[1] χ^2
	R	*r*	Total	
	Number	*Number*	*Number*	
8510	746	259	1,005	0.319
8512	763	272	1,035	.905
8514	260	58	318	7.753
8519	286	95	381	.001
9538	88	24	112	.762
Total	2,143	708	2,851	.042

[1] For each χ^2 there is 1 degree of freedom; $\chi^2 = 6.635$ indicates a discrepancy equal to the 1-percent level of significance (*14*).

Independent inheritance between self-fertility produced by S^f and the red hypocotyl factor *R* (*16*) is indicated in backcross populations (table 2). The observed distribution was 80 : 79 : 81 : 84, where the theoretically expected number, assuming independence between S^f and *R*, is 81 plants for each class. Independent inheritance between S^f and *R* is also shown by F_2 data (table 3). The F_2 populations were secured by selfing *R r* S^fS^x plants, where, if linkage is assumed, *R* and S^f entered in the coupling phase. In selfing heterozygous plants, S^fS^x, it has been shown (table 1) that, in general, only S^f pollen

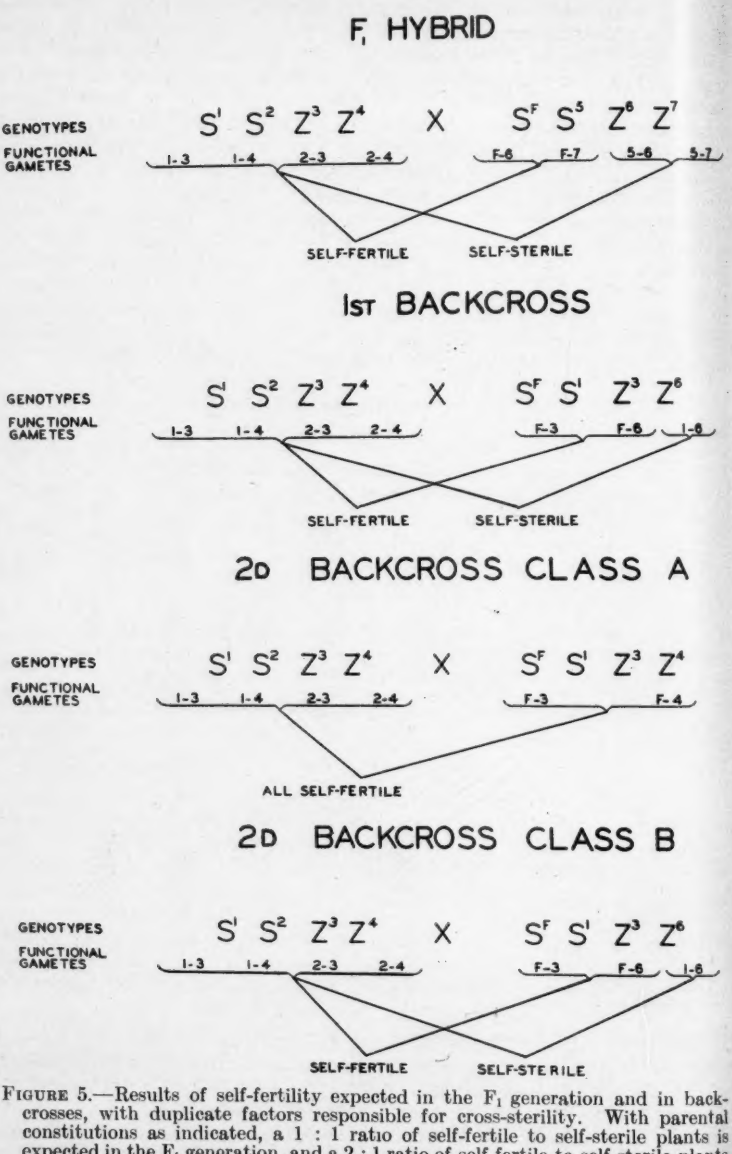

FIGURE 5.—Results of self-fertility expected in the F_1 generation and in backcrosses, with duplicate factors responsible for cross-sterility. With parental constitutions as indicated, a 1 : 1 ratio of self-fertile to self-sterile plants is expected in the F_1 generation, and a 2 : 1 ratio of self-fertile to self-sterile plants is expected in the first backcross. There are two types of populations in the second backcross generation: Class A, giving all self-fertiles; and class B, giving 2 : 1 ratios of self-fertile to self-sterile plants. Gametes are indicated by showing superscripts only, 1–3 representing gametes S^1Z^3, etc.

functions. Therefore, if R were completely linked with S^f all F_2 plants should have carried R and any significant amount of linkage would be revealed by a deficiency of r plants. In table 3, a deficiency of r plants is indicated for population 8514 (260 R:58 r plants), but the other 4 F_2 populations show normal 3:1 ratios. The combined results for the 5 populations show 2,143 R to 708 r plants, which is a good 3:1 ratio and indicates independence between S^f and R.

The presence of duplicate sterility factors is indicated by the behavior of successive backcrosses to the self-sterile clone 144 (table 4 and fig. 5). Clone 144, arbitrarily designated $S^1S^2Z^3Z^4$, was crossed with the self-fertile clone 70. Clone 70 proved to be heterozygous for self-fertility and, to illustrate theoretical assumptions, is assumed to be of constitution $S^fS^5Z^6Z^7$. Segregation was observed in the F_1 population with 4 self-fertile plants and 2 self-sterile plants (table 4). In the first backcross generation there were 11 self-fertile and 5 self-sterile plants. In the second backcross generation there were 52 self-fertile but no self-sterile plants. These results are all in agreement with expectation based on the assumption of duplicate sterility factors.

TABLE 4.—*Inheritance of self-fertility in successive backcrosses to self-sterile clone 144*

Hybrid or backcross	Population No.	Self-fertile plants	Self-sterile plants
		Number	*Number*
F_1 generation, $S^1S^2Z^3Z^4 \times S^fS^5Z^6Z^7$: Clone 144×clone 70	4514	4	2
First backcross, $S^1S^2Z^3Z^4 \times S^fS^1Z^3Z^6$: [1] Clone 144×4514–635	5247	11	5
Second backcross, $S^1S^2Z^3Z^4 \times S^fS^1Z^3Z^4$: [2] Clone 144×5247–3	6169	52	0

[1] $S^fS^1Z^3Z^6$ is 1 of 8 different self-fertile genotypes expected in the F_1, all of which, when used as pollen parents, produce 2 : 1 ratios of self-fertile to self-sterile offspring in the first backcross generation.

[2] $S^fS^1Z^3Z^4$ is 1 of 4 different self-fertile genotypes expected in the first backcross which, when used as pollen parents, produce nothing but self-fertile offspring in the second backcross. Four other genotypes, $S^fS^1Z^3Z^6$, etc., if used similarly, produce 2 : 1 ratios of self-fertile to self-sterile plants, as in the first backcross generation. (See fig. 5.)

The nature of expected results in successive backcrosses to a self-sterile plant is illustrated in figure 5. For convenience the self-sterile plant is assumed to be of constitution $S^1S^2Z^3Z^4$ and the original self-fertile pollen plant, $S^fS^5Z^6Z^7$. With a pollen parent of the type $S^fS^5Z^6Z^7$, heterozygous for S^f, a 1 : 1 ratio of self-fertile to self-sterile plants is expected in the F_1 generation. If the pollen parent were homozygous for S^f all F_1 plants would be self-fertile, but the type of results expected in backcrosses would remain the same.

Of the possible 16 different F_1 genotypes that may be derived from the parental gametes indicated in figure 5, eight ($S^fS^1Z^3Z^6$, $S^fS^1Z^4Z^6$, etc.) carry S^f and should be self-fertile. The behavior, with regard to segregation for self-fertility in successive backcrosses, is the same irrespective of which of the eight self-fertile genotypes is used as a pollen parent in the first backcross. Self-fertile F_1 plants produce four types of gametes. The F_1 $S^fS^1Z^3Z^6$, for instance, may produce S^fZ^3, S^fZ^6, S^1Z^3, and S^fZ^6 gametes, but S^1Z^3 pollen is expected to be sterile in a backcross to the maternal parent $S^1S^2Z^3Z^4$. The sterility of the S^1Z^3 class of pollen accounts for the 2 : 1 ratio of self-

fertile to self-sterile plants in the first backcross generation. In the second backcross generation two classes are expected, class A and class B (fig. 5). The theory requires that in class A all the offspring should be self-fertile and in class B there should be a 2:1 ratio for self-fertile to self-sterile plants. Class A and class B populations are expected with equal frequency.

Class A populations in the second backcross generation involve self-fertile pollen plants of the type $S^fS^1Z^3Z^4$ with three of the four genes in common with the self-sterile maternal parent $S^1S^2Z^3Z^4$. From $S^fS^1Z^3Z^4$ plants pollen carrying S^f is the only pollen that is functional with the $S^1S^2Z^3Z^4$ clone; hence, all the offspring carry S^f and are expected to be self-fertile. In table 4 it appears that the 52 self-fertile plants in the second backcross generation, population 6169, may be accounted for by the fact that it was of the class A type. The class B type of population, resembling the first backcross, is not represented in backcrosses to clone 144 (table 4).

Difficulty is encountered in attempting to explain backcrosses to clone 90 on the basis of duplicate factors for sterility. The results for these backcrosses are shown in table 5. Clone 90, rrS^aS^b, was first crossed with the self-fertile plant 2255–7, RRS^fS^f, and the resulting F_1 population was labeled 4356A. Clone 90 was then backcrossed through three generations to its own red self-fertile offspring (RrS^fS^a or RrS^fS^b).

TABLE 5.—*Inheritance of self-fertility in successive backcrosses to self-sterile clone 90*

Hybrid or backcross	Population No.	Self-fertile plants	Self-sterile plants
		Number	*Number*
F_1 generation, $S^aS^b \times S^fS^f$:[1]			
Clone 90×2255–7	4356A	7	0
First backcross populations, $S^aS^b \times S^fS^a$ (or S^fS^b):			
Clone 90×4356A–671	588	16	20
Clone 90×4356A–673	590	11	13
Total		27	33
Second backcross populations, $S^aS^b \times S^fS^a$ (or S^fS^b):			
Clone 90×590–17	6118	57	[2] 27
Clone 90×590–19	6119	13	12
Third backcross populations, $S^aS^b \times S^fS^a$ (or S^fS^b):			
Clone 90×6118	7128	23	[2] 5

[1] Evidence for a duplicate set of *Z* factors (table 4) considered in text, but, since all results with clone 90 backcrosses cannot be explained by duplicate factors, only the *S* series of factors is indicated here.
[2] Deficiency of self-sterile plants, as compared with the number of self-fertile plants, in populations 6118 and 7128, indicates selective action against S^a or S^b pollen.

In the first backcross generation a total of 60 plants was tested (populations 588 and 590, table 5) of which 27 were self-fertile and 33 were self-sterile, which is a good 1:1 ratio. This 1:1 ratio is not in agreement with expected results based upon the theory of duplicate sterility factors. A 2:1 ratio of self-fertile to self-sterile plants is expected with duplicate factors for sterility (fig. 5). Since a total of 60 plants were tested and 33 were observed to be self-sterile, there is a deviation of 13 from expectation, which is over 3 times the standard error of 3.65.

Results with population 6118, which represents a second backcross generation, show 57 self-fertile plants to 27 self-sterile plants, which is a good 2:1 ratio and agrees with results expected with duplicate factors for cross-sterility (fig. 5). Population 6119, however, which

is also a second generation backcross, produced 13 self-fertile to 12 self-sterile plants; hence, these results agree more closely with a 1:1 ratio.

Population 7128 represents a third backcross generation. Of 28 plants tested, 23 were self-fertile and 5 were self-sterile (table 5). The deficiency of self-sterile plants is too great to suggest a 2:1 ratio of self-fertile to self-sterile plants.

Since the backcross data with clone 90 do not clearly fall in line with the theory of duplicate factors, it is possible that some other auxiliary factors may be involved. All backcross data, however, both with clone 144 (table 4) and clone 90 (table 5), show that a single series of *S* factors cannot control cross-sterility. If a single series of *S* factors determined cross-sterility, all plants in the first backcrosses should have been self-fertile, because the maternal plants S^aS^b would have been sterile to the S^a (or S^b) pollen from F_1 $S'S^a$ (or $S'S^b$) plants. For S^a (or S^b) pollen to be effective in backcrosses to self-sterile parental clones, it is necessary to assume the presence of additional factors. The second and the third backcross generations represent a higher degree of inbreeding with a likelihood of greater similarity of genotypes between plants used for pollen parents and maternal parents. This closer approach to the genotype of the maternal parents may have been responsible for greater dependence upon the one allelic series of factors under investigation, with a greater deficiency of self-sterile plants in second and third backcross populations as indicated in tables 4 and 5.

Special attention was given to the 27 self-sterile plants in population 6118, a second backcross to clone 90 (table 5). Two of these 27 self-sterile plants produced aborted pollen. Nine of the self-sterile plants with normal pollen were subjected to further study. Clone 90, S^aS^b, was fully fertile to the pollen from seven of these nine plants of population 6118, assumed to be S^aS^a and S^aS^b (or S^bS^b and S^aS^b). Results with the seventh plant, G (table 6), were negative but questioned, and the eighth plant was not tested. Six of the self-sterile plants, A, B, D, G, H, and I (table 6), were fully fertile to pollen of clone 90, and three plants, C, E, and F, were rather poorly fertile. Thirteen pollinations between respective self-sterile plants of population 6118 were also attempted. Seven of these crosses were fertile, and combinations E×H and H×C were the only two definitely incompatible combinations discovered. None of the self-sterile genotypes in population 6118 (S^aS^a and S^aS^b or S^bS^b and S^aS^b) could be fertile in either direction with clone 90 (S^aS^b) if S^a and S^b alone determined cross-sterility. Apparently the presence of duplicate or auxiliary factors made it possible to secure plants homozygous for S^a and S^b.

TABLE 6.—*Compatibility of self-sterile segregates from the second backcross population 6118*

Clone 90 as parent	Compatibility [1] of self-sterile plants A to I in population 6118 with clone 90								
	A	B	C	D	E	F	G	H	I
Clone 90 as female	+	+	+	+	+	+	(2)	(2)	+
Clone 90 as pollen parent	+	+	P	+	P	P	+	+	+

[1] Designations: +=fertile; P=poorly fertile. [2] Results negative but questioned. [3] Not tested.

SELF-FERTILITY BY MUTATION FROM THE 12C STRAIN

The self-sterile clone 4, of the 12c strain, previously described and used extensively in connection with studies of cross-sterility, gave rise to a rather remarkable instance of self-fertility. Presumably the factor S^f for self-fertility arose from S^z by mutation.

FIGURE 6.—Beets under heavy curly top exposure with uniform soil fertility and cultural care. Photographed September 21, 1940, at Salt Lake City, Utah. *A*, Strain 1167, used extensively for source of self-fertility factor S^f; *B*, an S_3 population from clone 4 of the 12c strain, with self-fertility apparently derived by mutation; *C*, susceptible European variety R. & G. Old Type.

Four vigorous vegetative cuttings from clone 4 were planted in a city-garden isolation in Ogden, Utah, in 1933. These plants grew well and flowered normally, but very few of the flowers were fertilized and only a scant supply of poorly developed seed was produced. This small supply of seed was carefully planted in a greenhouse.

Twenty seedlings grew from this seed, but all were either red garden beet or Swiss chard hybrids, except four plants that resembled the parental plant, clone 4, and looked like sugar beets. The male parentage of these four plants was of course much in doubt. Since pollen from distant and unknown sources of red garden beets and Swiss chard reached the isolation, the four seedlings resembling sugar beets may also have arisen from hybridization with distant sources of sugar-beet pollen. Without knowing their male parentage, the four plants were grown to the flowering stage and their sterility reactions were studied. One of these plants was very exceptional because of a high degree of self-fertility.

Self-fertilized S_2 seed produced under paper bags was collected from this self-fertile plant. From this S_2 seed, 29 plants were grown and tested, and 28 were found to be highly self-fertile.

If this self-fertility arose from self-fertilization of clone 4, then mutation appears to be the only logical explanation. Certain facts indicate that the original self-fertile plant probably did arise by mutation rather than by contamination from a distant source of pollen. The curly top resistance and uniformity in bolting tendency of the offspring were factors furnishing conclusive evidence. Clone 4 was resistant to curly top but not so highly resistant as strain 1167. In 1933, when clone 4 plants were isolated at Ogden, curly top resistant varieties were not available to commercial growers; therefore, any sugar-beet pollen likely to have reached the isolation would have been from European varieties susceptible to curly top.

The S_2 population derived from selfing the original self-fertile plant showed a high degree of uniformity for a fast bolting tendency similar to that of clone 4. Twenty S_3 populations derived from selfing the S_2 plants were tested for curly top resistance in 1940. The degree of uniformity in leaf type and in curly top resistance was sufficient to rule out any possibility of origin through hybridization in the 1933 isolation with a susceptible variety. The S_3 plants in the 20 S_3 populations, when grown under a heavy curly top exposure, were remarkably uniform for the rather unusual leaf type and intermediate degree of curly top resistance shown in figure 6, *B*.

DISCUSSION

Any hypothesis to account for the observed results on self- and cross-sterility in sugar beets must involve some complexity. It was found necessary to assume the presence of duplicate oppositional factors to give a satisfactory explanation of the cross-sterility data. Unknown auxiliary factors apparently further complicated some of the results on cross-sterility. In contrast with the complexity of inheritance of cross-sterility, the inheritance of a high degree of self-fertility in sugar beets was found to be produced by the single factor S^f.

The simplicity of the inheritance of self-fertility is of much interest to the plant breeder. The knowledge that a single factor, S^f, produces self-fertility simplifies the problem of obtaining inbred lines. With only a single factor involved, it becomes a simple matter to transfer the self-fertility character to any material desired. As soon as the factor S^f is introduced, inbred lines can be easily produced under paper bags or by any other feasible means of isolation. This factor for self-fertility has been added to a wide variety of curly top resistant

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strains of sugar beets at the Salt Lake City laboratory of the Division of Sugar Plant Investigations.

The F_1 hybrids between self-sterile and self-fertile plants, heterozygous for the factor S^f, have shown a remarkably high degree of self-fertility. This increased self-fertility seems to be associated with hybrid vigor. Large quantities of pollen are produced by these vigorous F_1 plants. In several instances the degree of self-fertility apparently decreased with inbreeding. Sundelin (*30*) reported similar observations and made what appears to be a logical assumption that the apparent decrease in degree of self-fertility sometimes associated with continued inbreeding is caused by a general decrease in vigor. The inbred lines that lack vigor have been inclined to be slow to flower, thus encountering hotter and more unfavorable weather under field conditions. In some instances inbred lines have been very poor pollen producers.

Full utilization of self-fertility in breeding work, however, is dependent upon further information, because there are certain disadvantages in self-fertility when hybridization is desired. Recovery of self-sterility from self-fertile plants is not difficult as long as the factor S^f for self-fertility is held in the heterozygous condition. Hybrids between self-steriles S^aS^b and heterozygous self-fertiles S^fS^z yielded 50 percent self-steriles S^aS^z (or S^bS^z), and self-sterile segregates were easily identified by means of tests with paper bags. However, the maintenance of the factor S^f in the heterozygous condition requires continuous backcrossing to self-sterile plants, which may not be a practical procedure unless some simplified methods can be devised. Knowledge of linkage between the factor S^f and other Mendelian characters would be of particular interest. No linkage between the factor S^f and the factor R for red hypocotyl and plant color is indicated in data reported (tables 2 and 3).

The existence of intermediate or partly self-fertile types, which were largely avoided in the present studies, adds further complexity to genetic interpretations. Indications of embryo abortion associated with this partly self-fertile condition were observed in the Tracy strain 2769. These plants were not self-fertile, nor could they be considered as typically self-sterile. The pericarps of the seed balls under paper bags in the greenhouse swelled quickly after the flowers opened, a behavior similar to that of fully self-fertile plants, and the stigma lobes disintegrated quickly, making the use of paper bags impossible in the work of hybridization. Nevertheless, these plants produced nothing but empty seed balls, while known self-fertile plants under the same conditions produced good viable seed. From the limited observations made, it appeared that fertilization had probably been completed in many cases and that death of the embryo was the cause of these empty seed balls. These observations are in agreement with those of Kharechko-Savitskaĭa (*17*, *19*), who has described death of the beet embryo as a common result of self-fertilization. Brink and Cooper's (*5*) work on alfalfa indicates that death of the young embryo may commonly be associated with self-fertilization.

SUMMARY

The degree of self-sterility in *Beta vulgaris* L. was found to be determined by both environmental and heritable influences. Under greenhouse conditions end-season self-fertility was pronounced with

certain self-sterile plants. Intermediate types with a partly self-fertile condition, which was clearly heritable, were observed, but these types were avoided in attempting a genetic analysis of self-sterility and fertility.

Cross-sterility was found to be common in the curly top resistant line 12c. This cross-sterility was frequently nonreciprocal in behavior. An explanation based on a duplicate series of oppositional factors explains most of the results.

A highly self-fertile condition was produced by a single Mendelian factor designated S^f. The expression of the factor S^f was clearly defined; but identification of other S factors, believed associated with self-sterility and allelic to S^f, was difficult owing to the presence of unknown auxiliary factors or to duplicate factors that were not identified. Self-sterile plants were designated S^aS^b; and F_1 hybrids with self-fertiles, S^fS^a or S^fS^b. The S^a (or S^b) pollen did not produce self-fertilization on F_1 S^fS^a plants. The heterozygous S^fS^a plants bred true for self-fertility, presumably with the production of only S^fS^f and S^fS^a offspring. No linkage was detected between the factor S^f for self-fertility and the factor R for red plant and hypocotyl color. One instance is reported where self-fertility arose suddenly in a self-sterile line, presumably by mutation.

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GENETICS OF PSEUDO-SELF-COMPATIBILITY AND ITS RELATION TO CROSS-INCOMPATIBILITY IN TRIFOLIUM REPENS[1]

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INTRODUCTION

When a large number of white clover (*Trifolium repens* L.) plants, grown from open-pollinated seed, were self-pollinated under bag in the field (*3*),[2] a few were self-incompatible, a few others were as self-compatible as they were cross-compatible, but the large majority were intermediate, setting only a few seeds per head. This intermediate self-compatibility has been called "pseudo-self-compatibility" by previous workers, and the term will be used here in that general sense. Much variation has been found regularly in pseudo-self-compatibility, not only between plants but also within plants. No method has been found to eliminate the latter variation, but all mean values have been based on at least several heads. Williams (*8*) has described plants of white clover that set only a few seeds per head, but he did not report on the inheritance of this character. Since this ability of a plant to set selfed seeds, even though relatively low in self-compatibility, has obvious importance in a breeding program, it was desired to determine the genetic mechanism responsible and its relation to that causing self- and cross-incompatibility (*1*).

MATERIALS AND METHODS

The female parent of the *Trifolium repens* used in this investigation came from seed collected in Maryland, and the male parent from seed collected in New York. The cross between them was made in the winter of 1937–38, with clonal increases grown in the greenhouse. The F_1 population was planted in the field in 1938, the F_2 in 1939, and the F_3 in 1940. Every plant of the progeny has been similar to the two parents in having solid green leaves, the recessive condition to most of the common leaf markings found. The plants selected for greenhouse study were chosen principally for their vigor, good flowering, and freedom from disease. All crosses were made in screened greenhouses during the winter. The techniques used for emasculating and pollinating in the greenhouse, as well as for self-pollination under bag in the field, have already been described (*3*).

EXPERIMENTAL RESULTS

BEHAVIOR OF PARENT PLANTS

During their first summer in the field (1937) about one-half of the 10,000 plants in the nursery flowered. Over 200 of these were bagged, and the plant setting the highest number of seeds was chosen as the

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[2] Italic numbers in parentheses refer to Literature Cited, p. 709.

TABLE 1.—*Number of seeds set per 10 flowers in all possible reciprocal combinations between 13 pseudo-self-compatible sister plants (2–3 to 2–15) resulting from the previous cross between a pseudo-self-compatible female parent (2–1) and a self-incompatible male parent (2–2), together with the reciprocal backcrosses of each F_1 plant with both parents and the seed set by each of these plants under bag in the field*

Female parent			Seeds set [1] after pollination with indicated plant of group—																Selfed seeds per head in field in—	
Group No.	Genotype	Plant No.	2-I (S_4S_5)	2-II (S_5S_7)	2-III (S_4S_6)		2-IV (S_5S_6)				2-V (S_4S_7)				2-VI (S_6S_7)			Average for compatible crosses		
			2-1	2-2	2-9	2-12	2-3	2-7	2-11	2-14	2-4	2-6	2-10	2-13	2-5	2-8	2-15		1939	1940
																			No.	*No.*
2-I	S_4S_5	2-1	0	48	43	43	47	44	41	50	45	45	46	36	46	45	45	44.6	51.8	37.5
2-II	S_5S_7	2-2	53	1	53	56	55	52	55	54	50	57	50	[2] (57)	52	56	52	53.7	2.8	.9
2-III	S_4S_6	2-9	0	41	0	0	24	39	42	41	47	(45)	42	38	42	38	46	40.4	1.9	3.0
		[3] 2-12	0	46	1	0	46	45	40	48	42	(41)	44	47	49	47	49	45.3	5.0	10.4
2-IV	S_5S_6	2-3	35	29	37	26	[4] 1	0	0	1	40	28	22	33	(36)	39	36	32.8	21.0	-----
		2-7	41	32	38	42	0	0	0	[4] 2	45	50	45	42	44	46	36	41.9	6.7	13.2
		2-11	33	44	31	37	0	0	0	[4] 1	35	34	44	31	30	36	41	36.0	24.7	48.4
		[3] 2-14	34	36	33	32	0	0	[4] 1	[4] 2	36	(27)	39	32	27	36	32	33.1	-----	4.1
2-V	S_4S_7	2-4	0	(40)	48	48	37	53	48	51	0	0	0	0	42	49	39	45.5	-----	3.1
		[3] 2-6	0	46	(37)	38	42	37	42	46	[4] 1	0	0	0	38	36	48	41.0	11.1	7.6
		2-10	[4] 1	34	41	42	44	40	50	43	0	0	0	0	45	37	42	41.8	.9	8.3
		2-13	0	49	44	38	44	49	44	42	[4] 1	0	[4] 1	0	(49)	47	45	45.1	-----	-----
2-VI	S_6S_7	2-5	46	42	39	41	45	40	40	48	38	37	41	43	0	[4] 2	0	41.7	-----	-----
		[3] 2-8	37	34	30	40	31	39	(39)	44	(37)	38	31	38	0	0	0	36.5	13.0	19.3
		2-15	46	43	45	47	46	50	48	47	52	49	40	47	[4] 1	0	[4] 1	46.7	5.0	-----
Average of F_1																		40.8	9.8	13.1

[1] Values enclosed in heavy black lines are incompatible crosses or selfs.

[2] Numbers in parentheses in this and the following tables have been adjusted to a 10-flower basis. For instance, if a pod was lost at harvesting, the total number of seeds obtained was increased by ⅙. In most cases at least 8 flowers were available.

[3] Plants selected in each group as parents of the F_2 population.

[4] Duplicate cross yielded no seed.

female parent (plant 2–1 or group 2–I in all tables). The 2 heads enclosed at that time averaged 115 seeds per head. In the following winter in the greenhouse, the manipulated heads averaged 55.4 seeds, while the next summer in the field only 21.5 seeds per head were obtained. As shown in table 1, the averages for 1939 and 1940 were 51.8 and 37.5, respectively. With bee pollination under a cage (*3*), this plant averaged only 19.4 seeds per head. Although the interannual variation was very great, this parent appeared to represent an extreme type of pseudo-self-compatibility. Few other plants have averaged as many seeds per head without also giving evidence of true self-compatibility (*2*).

It should be noted that pseudo-self-compatibility is brought into expression only by manipulation of the heads. In the greenhouse during 1938–39, 10 flowers on 1 head of the female parent were selfed following emasculation, 2 similar heads were selfed without emasculation, and 1 was selfed in the bud. One of the unemasculated heads bore 4 seeds, but the others had none. Similar results were obtained with the F_1 and F_2 plants. When an abundance of pollen was placed on the stigma by hand in the greenhouse, these plants proved almost self-incompatible. Yet with the supposedly much less precise pollination resulting from rubbing of entire heads, the same plants showed a high degree of pseudo-self-compatibility. A similar behavior has been found with other unrelated pseudo-self-compatible plants. When a large amount of self pollen is placed on the stigma, the incompatibility reaction is so potent as to prevent almost all pollen tubes from growing through the style (*4*). On the other hand, it has been observed that with manipulation relatively few pollen grains adhere to the stigma. In this case, the incompatibility reaction may not be so strong, and there may be a better chance for fertilization.

The original male parent (plant 2–2 or group 2–II in all tables) yielded no seed when manipulated under bag in 1937. The following winter in the greenhouse it produced by manipulation only 1.5 seeds per head, but the next summer in the field it again produced no selfed seed. Similarly, in 1939 and 1940 its seed set was very low (table 1); comparatively speaking, this plant may be considered practically self-incompatible.

GENETICS OF CROSS-INCOMPATIBILITY AMONG PSEUDO-SELF-COMPATIBLE PLANTS

The seed set obtained when crossing reciprocally in all combinations the 13 selected F_1 plants and also the seed set from the reciprocal backcrosses to both parents are shown in table 1. Almost every cross was made twice and a few were made three times, the replicates usually being made by different persons, some on the same day and others at various intervals up to 7 weeks. Since the largest number of seeds obtained was considered the most accurate measure of the true potentialities of a combination, only the higher or highest seed set of the replicates is recorded in table 1. Lower numbers probably resulted from poor pollination or from damage during crossing and seed ripening rather than from reduced compatibility. Although replicates usually varied somewhat in number of seeds, it was generally not difficult to decide whether a particular head had been involved in a compatible or an incompatible mating, and in no case did replicates give different compatibility results. The average of the higher seed set among the compatible F_1 intercrosses was 40.8 per 10 flowers, whereas the average

obtained from 104 incompatible F_1 crosses and selfs, including replicates, was 0.18. About one-half of these seeds produced in the greenhouse from incompatible matings proved contaminants when a sample of them was tested for possible homozygosity. In other words, the average of the incompatible matings should really be about 0.09, which effectively doubles the ratio between compatible and incompatible crosses in average seed set.

Four intrasterile, interfertile groups of 4, 4, 3, and 2 plants, respectively, were found among the F_1 population. From this it can be inferred that cross-incompatibility among pseudo-self-compatible plants is determined by a series of multiple oppositional factors (*6*), and that the heterozygous parents used here differed in all four factors which they carried. According to this hypothesis, all backcrosses to both parents should be compatible in both directions. As shown in table 1, however, the backcrosses of two of the F_1 groups (2–III and 2–V) with the original female parent (2–I) as male were incompatible. This difference between reciprocal backcrosses can be explained best on the assumption that the plant involved (2–I) is homozygous for *S* factors; but, as already pointed out, it must originally have been heterozygous in order to yield four F_1 groups when crossed with 2–II. It is postulated, therefore, that subsequent to the original cross either a mutation occurred to make this plant homozygous or a contamination occurred in the field. The plant was perpetuated in the field as clonal slips between the time of the original cross and the time of the backcrosses with the F_1 plants. Since all other results with this plant have been interpreted best on the assumption that all supposed clones of the female parent were homozygous, the plant is so designated in tables 4 and 5.

Because the genetic explanation of cross-incompatibility among pseudo-self-compatible plants is similar to that for self-incompatible plants, it seemed desirable to determine whether any of the *S* factors in the plants used here were identical with those previously reported (*1*). The four homozygous genotypes obtained in the 2-series (see p. 704) were crossed as males (table 2) onto the six groups of the 1-series

TABLE 2.—*Number of seeds set per 10 flowers when the 4 homozygous plants of the 2-series were crossed onto the 6 groups of the 1-series*

Female parent		Seeds set [1] after pollination with plant of genotype—				
Group No.	Genotype	S_1S_1	S_2S_3	S_5S_6	S_7S_7	Average for compatible crosses
		Number	*Number*	*Number*	*Number*	*Number*
1–I	S_1S_2	52	51	47	43	48.2
1–II	S_3S_4	**0**	[2] 15	[2] 18	31	31.0
1–III	S_1S_3	38	40	37	38	38.2
1–IV	S_2S_3	52	51	56	51	52.5
1–V	S_1S_4	**0**	46	53	47	48.7
1–VI	S_2S_4	**1**	46	----	[2] 24	46.0

[1] Values enclosed in heavy black lines are incompatible crosses.
[2] Cross was recorded as compatible by reflection of pedicels on third day after pollination. This abnormally low seed set was omitted from average for plant.

described in a previous paper (*1*). The homozygous genotype that was incompatible with one parental (1–II) and two F_1 groups (1–V

and 1–VI) must have borne the gene common to these three groups, namely S_4. Since all other combinations were compatible, the other three factors in the 2-series must have been different from those in the 1-series, and they have been called S_5, S_6, and S_7. A second test confirmed these results. When four intrasterile, interfertile groups are found in an F_1 population, these four groups, together with those of the two parents, constitute the six possible combinations in pairs of the four genes brought together in the original cross. The second test, therefore, consisted of crossing in all combinations the six groups found in the 1-series (*1*) with those found in the 2-series. With the groups of the 2-series as female, all 36 combinations were compatible, but with the 1-series as female, three of the 36 combinations failed. These involved the matings of 2–I as male with one parental (1–II) and two F_1 groups (1–V and 1–VI) of the 1-series. Here again, reciprocal matings are different, and they provide evidence not only that one gene of the 2-series must be the same as one in the 1-series, but that the particular gene is homozygous in the parent plant 2–I.

In order to assign genotypes to the six groups and to test further the hypotheses used to explain the reaction of 2–I, an F_2 test was carried out similar to that with the 1-series (*1*). Three F_1 intercrosses, involving matings of one of the F_1 groups as female with each of the other three, were selected for further test. In the case of the 1-series, a gene from each parent was arbitrarily assigned to one of the F_1 groups, and the other three groups were defined by their reaction with this first group. Here, however, one of the genes, S_4, is already defined because of its previous designation in the 1-series. Since the group used as female in these crosses did not bear S_4 (see reaction of 2–I in table 1), this group must have borne the other gene from the original female, together with one from its male parent. The genes assigned to this group were S_5 and S_6, and it has been called group 2–IV. The genotypes of the 2-series are as follows:

$$\begin{array}{cc} \text{(I)} & \text{(II)} \\ S_4S_5 & \times S_6S_7 \end{array}$$

$$\downarrow$$

$$\begin{array}{cccc} \text{(III)} & \text{(IV)} & \text{(V)} & \text{(VI)} \\ S_4S_6 & + S_5S_6 + & S_4S_7 + & S_5S_7 \end{array}$$

The three F_1 intercrosses should then yield as follows:

$$\begin{array}{cccc} \text{(IV)} & \text{(III)} & & \text{(I)} \quad \text{(III)} \\ S_5S_6 & \times S_4S_6 & \longrightarrow & S_4S_5 + S_4S_6 \end{array}$$

$$\begin{array}{cccc} \text{(IV)} & \text{(V)} & & \text{(I)} \quad \text{(III)} \quad \text{(VI)} \quad \text{(II)} \\ S_5S_6 & \times S_4S_7 & \longrightarrow & S_4S_5 + S_4S_6 + S_5S_7 + S_6S_7 \end{array}$$

$$\begin{array}{cccc} \text{(IV)} & \text{(VI)} & & \text{(VI)} \quad \text{(II)} \\ S_5S_6 & \times S_5S_7 & \longrightarrow & S_5S_7 + S_6S_7 \end{array}$$

When 38 F_2 plants were tested by backcrossing to the P and F_1 groups, only expected groups were obtained (table 3). This confirms the diploid personate theory of multiple oppositional factors as an explanation of cross-incompatibility among pseudo-self-compatible plants of white clover. Although the segregating progenies were small, the agreement between expected and obtained ratios was satisfactory

TABLE 3.—*Segregations of intrasterile, interfertile groups in F_1 and F_2*

Cross	Generation	Plants in group— 2-I Expected	2-I Obtained	2-II Expected	2-II Obtained	2-III Expected	2-III Obtained	2-IV Expected	2-IV Obtained	2-V Expected	2-V Obtained	2-VI Expected	2-VI Obtained	Total plants Expected	Total plants Obtained
		No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
2-I×2-II	F_1	-----	-----	-----	-----	3.25	2	3.25	4	3.25	4	3.25	3	13	13
2-IV×2-III	F_2	5	5	-----	-----	5	5	-----	-----	-----	-----	-----	-----	10	10
2-IV×2-V	F_2	4.5	4	4.5	5	4.5	4	-----	-----	-----	-----	4.5	5	18	18
2-IV×2-VI	F_2	-----	-----	5	6	-----	-----	-----	-----	-----	-----	5	4	10	10

in every case. Not all possible reciprocal combinations between F_2 plants and the 6 test groups were made, but there were enough crosses with every plant to be certain of its genotype. The reflection of the pedicels (*1*) was a good measure of compatibility with these plants, so that few of the F_2 crosses were made in duplicate. Here, as with the F_1 plants, no difficulty was generally experienced in distinguishing compatible from incompatible crosses. Since the data are similar to those obtained with self-incompatible plants (*1*), seed set is shown from only 4 F_2 plants (table 4). The types of behavior shown here are characteristic of those obtained with all 38 F_2 plants.

TABLE 4.—*Number of seeds set per 10 flowers when typical F_2 plants from cross 2-IV×2-V (2-14×2-6) were backcrossed to P and F_1 groups*

Group No.	Genotype	Plant No.	As female or male parent	Seeds set after backcrossing to group— 2-I (S_1S_4)	2-II (S_4S_7)	2-III (S_1S_6)	2-IV (S_6S_8)	2-V (S_1S_7)	2-VI (S_6S_7)
				Number	*Number*	*Number*	*Number*	*Number*	*Number*
"Recovered" 2-I	S_4S_5	2-31	♀	[0]	42	33	47	43	41
			♂	37	43	49	9	35	38
2-II	S_6S_7	2-124	♀	34	[0]	39	(32)	33	39
			♂	33	[0]	44	32	35	32
2-III	S_1S_6	2-128	♀	[0]	28	[0]	-----	30	39
			♂	40	38	[3]	23	25	25
2-VI	S_6S_7	2-129	♀	45	40	20	24	47	[0]
			♂	27	49	31	39	39	[0]

[1] Values enclosed in heavy black lines are incompatible crosses.

As stated, a few seeds were obtained from the incompatible crosses or selfs made with 10 flowers per head in the greenhouse, but considerably more were obtained from manipulation of entire heads, either in greenhouse or field. Representative individuals from these seeds were selected to be tested for homozygosity in the greenhouse by backcrossing to the P and F_1 groups. The reaction of 4 typical homozygous plants is shown in table 5. Altogether, 41 plants were included in this test; 12 were found to be homozygous, 18 heterozygous, and 11 contaminants. This is a lower proportion of contaminants than was obtained with self-incompatible plants (*1*). The contaminants had genotypes that could not be accounted for on the basis of their parentage and they probably arose from accidental cross-pollinations. It

should be noted that no similar contaminations were found in the F_1 or F_2 plants, indicating that the chances of error in compatible crosses are considerably less than with incompatible matings.

TABLE 5.—*Number of seeds set per 10 flowers when typical homozygous plants were backcrossed to P and F_1 groups*

Genotype	Plant No.	Parent group	Origin [1]	As female or male parent	Seeds set [2] after backcrossing to group—					
					2-I (S_4S_4)	2-II (S_4S_7)	2-III (S_4S_6)	2-IV (S_4S_5)	2-V (S_4S_7)	2-VI (S_4S_7)
					Number	*Number*	*Number*	*Number*	*Number*	*Number*
S_4S_4	2-77	III	A	♀	0	34	42	33	48	42
				♂	0	38	0	34	0	41
S_4S_5	2-62	IV	B	♀	51	(51)	42	49	52	36
				♂	53	54	37	1	35	0
S_4S_6	2-54	IV	C	♀	15	15	9	14	16	25
				♂	53	0	0	0	29	14
S_7S_7	2-52	VI	D	♀	45	45	41	40	37	21
				♂	46	0	44	30	0	1

[1] A=Self-pollination under bag in the field; B=entire head manipulated in greenhouse; C=selfing 10 flowers without emasculation in greenhouse; D=selfing 10 flowers after emasculation in greenhouse.
[2] Values enclosed in heavy black lines are incompatible crosses.

Additional proof of the assumption that 2–I had changed from S_4S_5 to S_4S_4 between the time of the original cross and the time of the F_1 backcrosses was obtained from the F_2 and homozygous plants. The F_2 plant 2–31 (table 4) is typical of the "recovered 2–I" (S_4S_5) genotypes inasmuch as it was incompatible as a female but compatible as a male with the original female parent. On the other hand, all 2–III plants in the F_2 failed not only reciprocally with group 2–III but also as female with group 2–I (table 4). The plants homozygous for S_4 failed in both directions with 2–I instead of only as males, and the S_5S_5 plants were compatible as male with 2–I when it was expected that they would be incompatible (table 5). Similar results were obtained when one F_3 progeny was tested. The seed used was that obtained from backcrossing the "recovered" S_4S_5 genotype as male onto the clones of the original female parent 2–I (table 4). When 10 of the F_3 plants were crossed reciprocally with plants of the "recovered" S_4S_5 genotype, all matings proved incompatible. These same plants, however, were compatible as males but incompatible as females with the original female parent 2–I. The anomalous behavior of all these plants, involving the failure of certain matings when they were expected to be compatible and the compatibility of others when they were expected to fail, can be explained in the same way as the incompatible F_1 backcrosses, simply by supposing that the clone used as 2–I in these tests was S_4S_4 instead of S_4S_5.

GENETICS OF PSEUDO-SELF-COMPATIBILITY

In both 1939 and 1940 the average seed set of the F_1 population was intermediate between those of the two parents (table 1). Also, in both years, a wide range was obtained in the averages of the individual F_1 plants. When the entire F_1 population (23 plants) was bagged in 1939, an average of 10.4 seeds per head was obtained

(table 6), while the individual plant averages ranged from 0.9 to 36.1. In 1940, only 9 F_1 plants were bagged, but their averages ranged from 3.0 to 48.4 seeds per head. Seven of these plants were selfed both years, and there was a significant interannual correlation ($r=0.867$, $P=0.02$–0.01) between the two groups of averages. It should be noted that at least one of the F_1 plants approached the pseudo-self-compatible parent in ability to set seed.

TABLE 6.—*Seed set in field of F_1, F_2, and backcross generation plants*

Cross	Generation	Percentage of plants with indicated number of seeds per head											Total number of plants	Mean number of seeds and standard deviation
		0–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	50+		
2-1×2-2	F_1	26	30	17	9	13			4				23	10.4±1.9
2-14×2-12	F_2	76	20	4									25	3.1± .6
2-14×2-6	F_2	61	32	7									28	4.2± .6
2-14×2-8	F_2	64	12	10	6	4	2	2					50	6.3±1.1
Total	F_2	66	19	8	3	2	1	1					103	4.9± .6
2-1×2-12	B	37	20	15	9	7	7	2	4				46	11.0±1.4
2-1×2-14	B	64	18	5	5	5				5			22	7.1±2.0
2-1×2-6	B	71	21	4				4					28	4.8±1.2
2-1×2-8	B	22	30	4	22	7	7		4			4	27	13.9±2.5
Total	B	46	22	8	9	5	4	2	2	1	0	1	123	9.5± .9

The four F_1 plants used as parents of the F_2 generation showed considerable difference in seed-setting ability. Since one F_1 plant was common to the three F_1 intercrosses, any differences in the F_2 populations might be attributed mainly to the nonrecurrent F_1 plants. When the significance of the difference between means of the separate F_2 populations was measured by the t test, values exceeding those where $P=0.05$ were obtained in one case. The averages of the three F_2 populations appear to be related to the average of their respective nonrecurrent F_1 parent, and a highly significant difference was found between the average of the entire F_2 population and that of the F_1.

By the t test, highly significant differences between the individual backcross populations were found. Also, the difference between the average of the total backcross population and of the entire F_2 population was highly significant, but the difference between the average of the backcrosses and of the F_1 was not significant. More plants setting a large number of seeds per head, like the original pseudo-self-compatible parent, were recovered in the backcross progeny than in the F_2. From the frequency distributions and standard errors in table 6 it can be seen that large variations between the individual plant averages were found in every population and that all distribution curves were positively skewed. All these data suggest that pseudo-self-compatibility is a quantitative character, probably determined by several additive genes, some of which were heterozygous in the parents.

RELATION BETWEEN PSEUDO-SELF-COMPATIBILITY AND CROSS-INCOMPATIBILITY

Almost all F_1 and F_2 plants whose incompatibility groups were determined in the greenhouse were selfed under bag in the field. These comparative data for the F_1 are shown in table 1. Plants of both relatively high and low pseudo-self-compatibility were found in each of the four F_1 groups. It might appear that the plants in groups 2–IV and 2–VI, both of which bear S_5, were higher in pseudo-self-

compatibility than those in groups 2–III and 2–V, neither of which bears S_5. This relationship did not hold, however, in the F_2. Three plants setting over 10 seeds per head were found in group 2–VI, but no such plants were obtained in the recovered 2–I group, which also bore S_5. Apparently little if any relationship exists between the S factors and the amount of pseudo-self-compatibility.

NUMBER OF SEEDS PER POD

It was previously concluded (*1*) that the number of ovules per ovary is a heritable character that may have practical importance. Additional information on this subject has been obtained with these pseudo-self-compatible plants. The number of seeds per pod resulting from controlled cross-fertilization of 10 flowers per head was used as a measure of the number of ovules. Probably the most reliable data are shown in table 1, where the largest numbers of crosses per plant are recorded and where almost all crosses were made originally in duplicate. The original female parent, 2–1, averaged 44.6 seeds per head, while the male parent, 2–2, averaged 53.7. The F_1 averaged 40.8, and individual plants ranged from 32.8 to 46.7. When 4 of these clones, together with the 2 parental plants, were used as female in the F_2 and homozygous tests, an interannual correlation ($r=0.938$, $P<0.01$) was observed in their average seed-setting ability. Few crosses were made in duplicate in the F_2, so the averages of these plants are probably not as accurate as those of the F_1, but in general the averages of the different F_2 populations appeared to be related to the average of their nonrecurrent F_1 parent. The data indicate that this character is probably determined by several genes for which the parents were heterozygous.

DISCUSSION

The literature dealing with incompatibility has been reviewed recently by Stout (*7*). According to his terminology, the kind of cross-incompatibility observed here is determined by oppositional allelomorphs of the diploid personate type. This sort of inheritance has been reported for many species, but in most cases the plants have been self-incompatible rather than pseudo-self-compatible. Since this pseudo-self-compatibility was expressed only when the heads were manipulated, cross-incompatibility could be studied in these plants as easily as in self-incompatible individuals. The study was facilitated because the differences in seed set between compatible and incompatible crosses were generally distinct and because in every case the reflexing of the pedicels provided a check on the seed set.

Here, as with the self-incompatible plants of white clover (*1*), a disomic segregation among the S factors was observed. White clover, however, is a tetraploid with 32 somatic chromosomes. The original male parent in this study was included among the plants studied at meiosis (*5*), where 16 bivalents were found regularly, and root tips from representative F_1 plants all showed 32 chromosomes. Root tips from the 2–I clone, which apparently had changed to S_4S_4, were examined cytologically, but no irregularities in its 32 chromosomes were observed. These observations support the previous conclusion (*1*) that the oppositional allelomorphs causing cross-incompatibility are present in only 1 of the 2 genomes found in white clover.

Four allelomorphs were found in the self-incompatible plants studied

for cross-incompatibility (*1*), and three additional factors were found in the parent plants used in this study. These seven genes have been obtained in homozygous condition, and all have been identified. It appears significant that seven of the eight genes borne by the four unrelated parents were different. The factor S_4, common to the two series, occurred in one case in a plant from Maryland seed and in the other in a plant isolated clonally from a pasture in central Pennsylvania. The evidence obtained in these investigations, together with that from several other sources, has led to the conclusion that a great many allelomorphs must be present in the series conditioning cross-incompatibility in white clover. In breeding experiments in which unrelated plants were used, the probability of cross-incompatibilities has been found to be very low. If the plants had been closely related, however, incompatibilities would have occurred much more frequently. It has been observed in other studies that the inbreds from pseudo-self-compatible plants may be homozygous for *S* factors. An F_1 between two such inbred lines might consist of a single intrasterile, interfertile group, in which case subsequent inbred generations would have to be derived by selfing rather than by intercrossing.

Several causes for pseudo-self-compatibility have been postulated—see review by Stout (*7*)—but in most plants it apparently is conditioned primarily by environmental conditions rather than by hereditary factors. In these plants of white clover, a complex hereditary mechanism for pseudo-self-compatibility has been demonstrated, but this ability to set selfed seed is apparently modified by the environment. Pseudo-self-compatibility is evidently not a case of "reduced seeding" in self-compatible plants, although part of the variation must be attributed to a reduction in seed set due to environmental conditions.

Pseudo-self-compatibility may be useful in a breeding program. Inbred lines may be obtained that tend to outcross instead of self when subjected to open-pollination. In this case, hybrid seed would be produced very easily. (This phase of the problem is now being investigated.) Likewise, if the F_1 consisted of a single genotype as the result of crossing two inbreds homozygous for five factors, sib mating would be prevented among the F_1 and four-way hybrids could be produced easily. In some respects, obtaining inbreds by means of pseudo-self-compatibility might be more desirable than using an S_f factor (*2*), since the latter might necessitate selecting only plants heterozygous for S_f in order to recover self-incompatible individuals at the end of the inbreeding. The usefulness of the type of pseudo-self-compatibility described will also depend on the ease with which it can be transmitted and selected for, but the present investigation only partially answers these questions.

SUMMARY

The original female parent of the *Trifolium repens* plants used in this study set a large number of selfed seeds when entire heads were manipulated, but it failed to set seed when 10 flowers per head were self-pollinated by hand in the greenhouse. The male parent was self-incompatible.

The pseudo-self-compatibility of the female parent was transmitted to the F_1, F_2, and backcross generation plants; it appears to be conditioned by several genes, which were additive in effect and heterozygous in the parents.

Four intrasterile, interfertile groups of 4, 4, 3, and 2 plants, respectively, were found among the F_1 plants. The compatible F_1 intercrosses averaged 40.8 seeds per 10 flowers, whereas the incompatibles averaged only 0.18. Reflection of the pedicels also was used to distinguish compatible from incompatible crosses.

The diploid personate theory of oppositional allelomorphs explains these cross-incompatibilities if it is assumed that the parents differed in all four factors which they carried.

When a further test was made by backcrossing 38 selected F_2 plants to the two parental and four F_1 groups, only the expected groups were obtained. In this way a certain genotype was assigned to each group, and the oppositional-factor hypothesis was confirmed for these pseudo-self-compatible plants.

Out of 41 plants resulting from incompatible crosses or selfs, 12 proved homozygous, 18 heterozygous, and 11 contaminants. Among the 12 were the 4 possible homozygous genotypes. One of the *S* genes from the pseudo-self-compatible parent was identical with the S_4 previously isolated from a self-incompatible plant.

When the original female parent was backcrossed with the F_1, F_2, and homozygous plants, certain combinations failed where they were expected to be compatible, and others were compatible where they were expected to fail. All of these results are explicable if it is assumed that this original parent changed from S_4S_5 to S_4S_4 subsequent to the original cross. This change could have resulted from either mutation or contamination in the field.

Since plants of both relatively high and low pseudo-self-compatibility were found in each of the six groups, it is evident that little relationship exists between the *S* factors and those conditioning the ability to set some selfed seed after manipulation.

It is pointed out that pseudo-self-compatibility may be useful in a breeding program.

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RELATIVE SUSCEPTIBILITY TO PYTHIUM ROOT ROT OF TWELVE DENT CORN INBREDS [1]

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INTRODUCTION

This paper presents the results of 2 tests of the relative susceptibility to pythium root rot (*Pythium arrhenomanes* Drechs.) of 12 inbred lines of dent corn (*Zea mays* L.).

Pythium arrhenomanes was first described by Drechsler [2] in 1928 as causing root rot of corn in Wisconsin and Illinois. The disease was first referred to by Johann et al.[3] in 1926 and more fully described in 1928.[4] The recent work of Rands and Dopp [5] has shown that the strains of *Pythium* that cause root rot of corn in Wisconsin, Illinois, Kentucky, Missouri, and other parts of the Corn Belt; root rot of wheat (*Triticum aestivum* L.) and other cereals in Canada; of pineapple (*Ananas sativus* Schult.) in Hawaii; and of sugarcane (*Saccharum officinarum* L.) in the southern United States, the Philippines, Hawaii, and other countries, all belong to one species, *P. arrhenomanes*, which is apparently a fungus of wide host range and of almost universal distribution.

Recent reports of root rot in the field and specimens of inbred and open-pollinated field corn from Iowa and Nebraska, from which *Pythium arrhenomanes* was isolated, have indicated that this root rot continues to have an important effect on the yield of field corn. Because of the wide distribution of this fungus and the rapidly increasing acreage of hybrid corn throughout the Corn Belt, it becomes increasingly important to learn more of the relative susceptibility to pythium root rot of the inbred parent lines in use at the present time.

The results of two greenhouse tests are given here as a measure of possible field damage.

MATERIAL AND METHODS

Seed [6] of 12 inbred lines of dent corn was washed for 10 minutes in a 1 : 1,000 solution of bichloride of mercury ($HgCl_2$), thoroughly rinsed in distilled water, and germinated on moist filter paper in Petri dishes. Each of the young seedlings was transferred to a 6-inch pot coated with asphaltum, and was allowed to grow 4 to 6 inches high

[1] Received for publication October 11, 1941.

[2] DRECHSLER, CHARLES. PYTHIUM ARRHENOMANES N. SP., A PARASITE CAUSING MAIZE ROOT ROT. Phytopathology 18: 873-875. 1928.

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[5] RANDS, R. D., and DOPP, ERNEST. VARIABILITY IN PYTHIUM ARRHENOMANES IN RELATION TO ROOT ROT OF SUGARCANE AND CORN. Jour. Agr. Res. 49: 180-221, illus. 1934.

[6] Supplied by M. T. Jenkins, of the Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.

before inoculations were made. By inoculating the plants after they were several inches high, seedling injury was avoided. In order to eliminate some of the sources of variability and to obtain more or less reproducible results, the plants were grown in clean quartz sand that had been heated for 6 hours at 15 pounds' pressure. The plants were watered once or twice a week with a nutrient solution containing the following salts in the partial volume (molecular concentration) indicated: Ammonium nitrate (NH_4NO_3), 0.004; monopotassium phosphate (KH_2PO_4), 0.0015; dipotassium phosphate (K_2HPO_4), 0.0005; magnesium sulfate ($MgSO_4$), 0.001; and calcium chloride ($CaCl_2$), 0.003; and trace elements (p. p. m.): Manganese (Mn), 5; aluminum (Al), 0.56; zinc (Zn), 0.25; boron (B), 0.53; copper (Cu), 0.25; and bromine (Br), 0.26. Before sterilization, iron was added to the quartz sand in the form of iron magnetite sand, 1 percent by weight. Greenhouse temperatures were maintained as low as would permit of good growth, and between the additions of nutrient solution the sand was kept moist by watering.

Plants of the 12 inbred lines of dent corn were inoculated in the greenhouse at the Arlington Experiment Farm, Arlington, Va. The culture of *Pythium arrhenomanes*[7] used in making the inoculations had been isolated in August 1939 from an open-pollinated variety, St. Charles White, from York, Nebr. The diseased plants were 4 to 5 feet in height and showed typical rotting of the smaller roots.

There were 10 controls of each inbred in each of the tests and 10 replicates of each were inoculated. The plants were set at random in the greenhouse benches, the controls on one bench and the inoculated plants on a parallel bench. Inoculations were made by placing squares (1 cm.^{2}) of corn meal-carrot agar cultures in the sand on either side of the plant. Sterile media were used for the controls. Measurements of the height of individual plants were made the day the plants were inoculated and every seventh day thereafter. At the end of the experiment the tops of the plants were cut off just above the roots and weighed. The roots were washed free of sand and weighed.

RESULTS

In the 1940 test, the corn plants grew for 4 weeks after inoculation with *Pythium arrhenomanes*. Figure 1 shows the differences in size at the end of the experiment of inoculated and uninoculated plants of typical inbreds.

Figure 2, *B*, shows the extent of root damage in the inbred Ia. L317 (fig. 1, *A*), which was the most resistant to root rot; and figure 3, *B* and *C*, the root damage in the inbred C. I.[8] 1 (fig. 1, *F*), which was the most susceptible. In these inoculated plants, the fine roots have been destroyed and even the larger roots show rotting. The root systems of the inbreds not illustrated also showed abundant fine roots in the controls and almost none in the inoculated plants. Because of high temperatures, the experiment was terminated after 4 weeks.

In the 1941 inoculation experiment, the plants grew for 7 weeks after inoculation. Differences were greater between uninoculated and inoculated plants, as shown in figure 4. But Ia. L317 continued to

[7] Identified by Charles Drechsler, of the Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.

[8] C. I. refers to accession number of the Division of Cereal Crops and Diseases. Formerly accession numbers for the inbred lines developed in this Division were designated by the prefix "U. S." instead of "C. I.," but they have recently been changed to avoid confusion with the designation of U. S. hybrids.

be the most resistant to *Pythium arrhenomanes* and C. I. 1 the most susceptible. The contrast between the bench of control plants and the bench of inoculated plants (fig. 5) gives some idea of the differences in growth. In figure 5, *B*, inoculated plants of Ill. R4, next to the steam pipes, grew much larger and more normally than in other positions on this bench. This was due to the higher temperatures and more rapid drying of the sand in these pots, both of which conditions are unfavorable for the development of *P. arrhenomanes*.

In both experiments, *Pythium arrhenomanes* destroyed most of the fine roots of all the inbred lines. In the more resistant inbred lines,

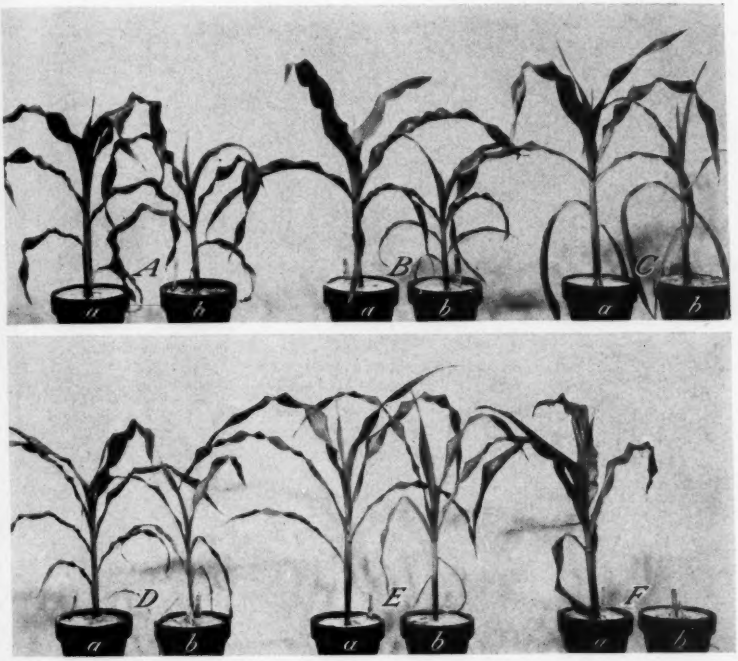

FIGURE 1.—Dent corn inbreds grown in sand plus nutrient solution, uninoculated and inoculated with *Pythium arrhenomanes* April 1, and photographed May 1, 1940: *A*, Ia. L317; *B*, Ia. Bl 345; *C*, Ia. Mc 401; *D*, C. I. 540; *E*, Ind. Tr; *F*, C. I. 1. *a*, Uninoculated; *b*, inoculated.

more of the larger roots were developed than in the susceptible ones.

The results of the 2 inoculation experiments on all 12 inbreds are given in tables 1 and 2. Table 1 shows the mean weekly height of inoculated and control plants, beginning at the time of inoculation, and weekly differences in growth in each inbred. Graphs in figures 6 and 7 show the mean weekly values in 1941 for some of the inbreds, illustrated in figure 4. The fungus interfered much less with the growth of inbreds Ia. L317 and Ia. Mc 401 than with that of Ind. Tr and C. I. 1. Ia. L317 showed the least susceptibility to attack and C. I. 1 the greatest susceptibility. This is shown not only in growth

of tops but in green weight of tops and roots as compared with controls.

The weekly figures in table 1 are summarized in table 2, which gives the total growth in centimeters of inoculated and uninoculated plants of each inbred, and the differences in growth between the inoculated

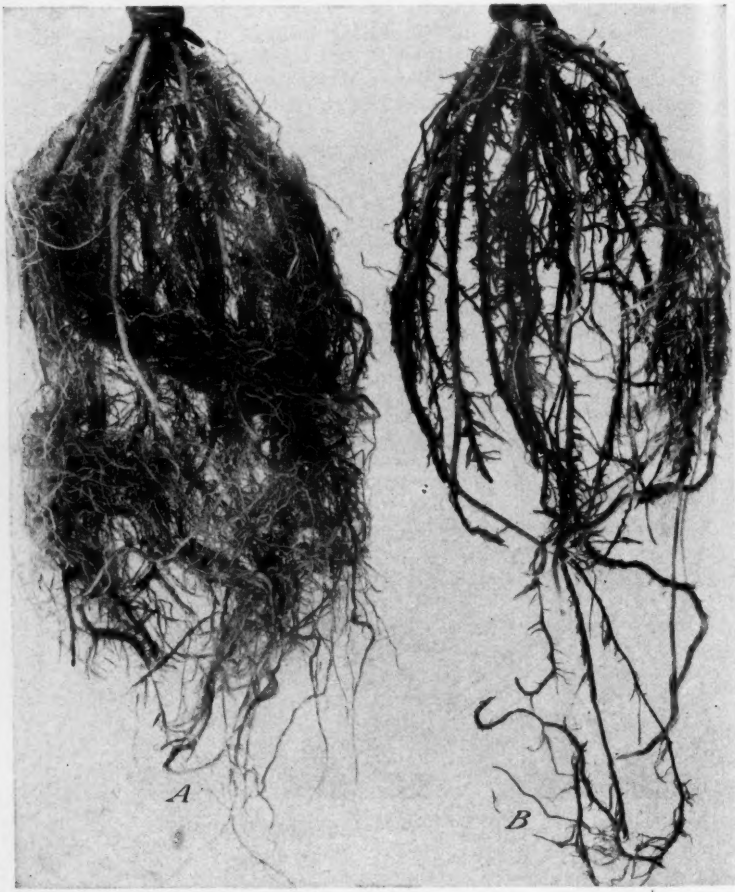

FIGURE 2.—Roots of dent corn inbred Ia. L317 grown in sand plus nutrient solution: *A*, Uninoculated; *B*, inoculated with *Pythium arrhenomanes* April 1, 1940. Photographed May 2, 1940.

and uninoculated plants of each inbred, in centimeters and in percentages of control plants. In column 1, all 12 inbreds show some reduction in growth owing to inoculation with *Pythium arrhenomanes*, but the amount of decrease varies with the inbred. The inbreds are arranged in the order of increasing percentage reduction in growth in 1940 (column 3). In columns 2 and 5 these differences are expressed in centimeters as a measure of the resistance of the different inbreds to inoculation with *P. arrhenomanes*.

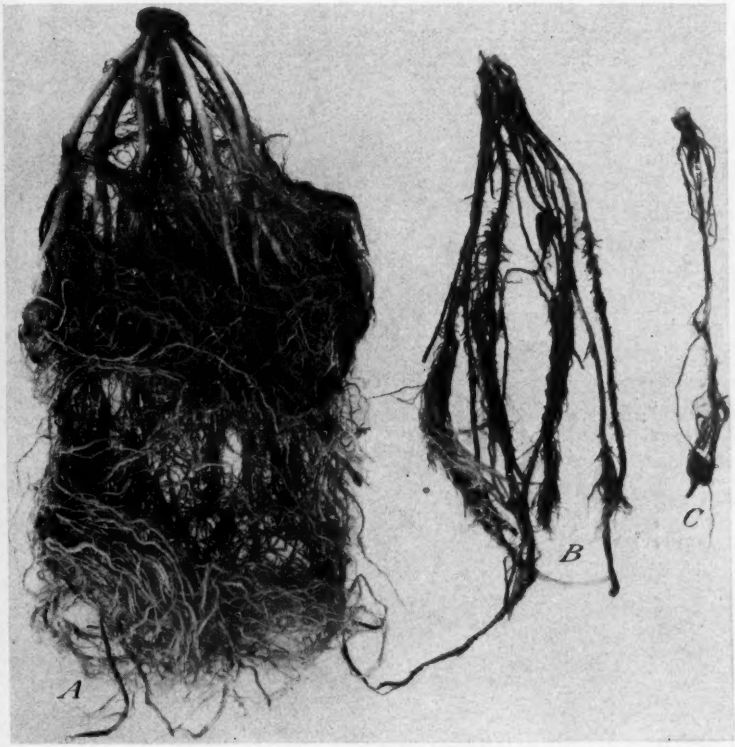

FIGURE 3.—Roots of dent corn inbred C. I. 1 grown in sand plus nutrient solution: *A*, Uninoculated; *B* and *C*, inoculated with *Pythium arrhenomanes* April 1, 1940. Photographed May 2, 1940.

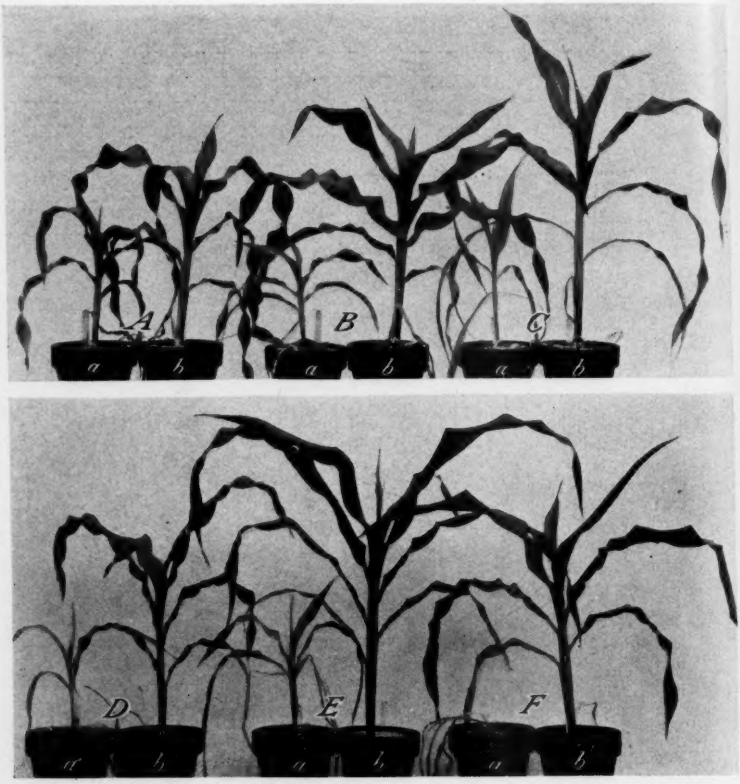

FIGURE 4.—Dent corn inbreds grown in sand plus nutrient solution, uninoculated and inoculated with *Pythium arrhenomanes* February 3, and photographed March 25, 1941: *A*, Ia. L317; *B*, Ia. Bl 345; *C*, Ia. Mc 401; *D*, C. I. 540; *E*, Ind. Tr; *F*, C. I. 1. *a*, Inoculated; *b*, uninoculated.

FIGURE 5.—Twelve dent corn inbreds grown in sand plus nutrient solution, Arlington Experiment Farm. Planted January 21, 1941. *A*, Uninoculated; *B*, inoculated with *Pythium arrhenomanes* February 3, 1941. Photographed March 25, 1941.

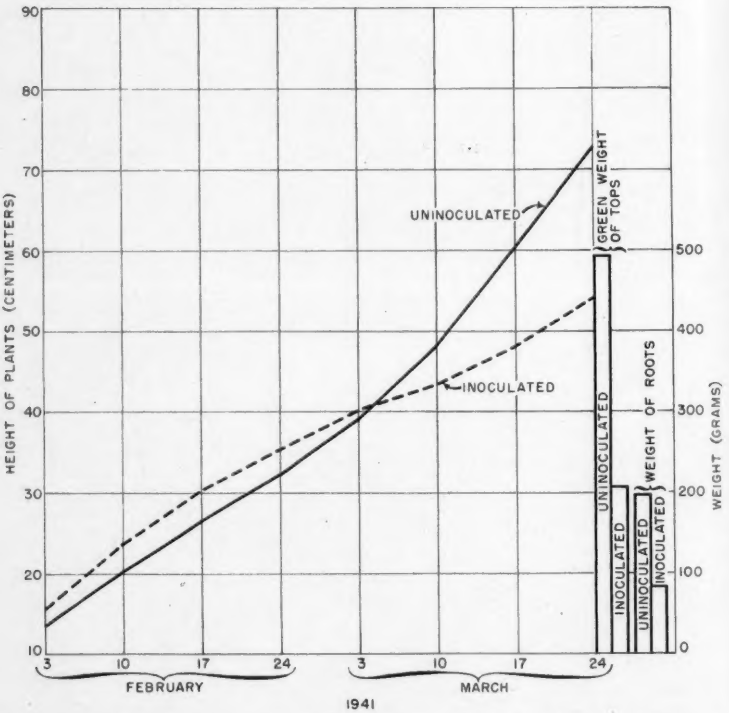

FIGURE 6.—Growth and green weight of tops and weight of roots of plants of dent corn inbred Ia. L317, uninoculated and inoculated with *Pythium arrhenomanes*, Arlington Experiment Farm, 1941.

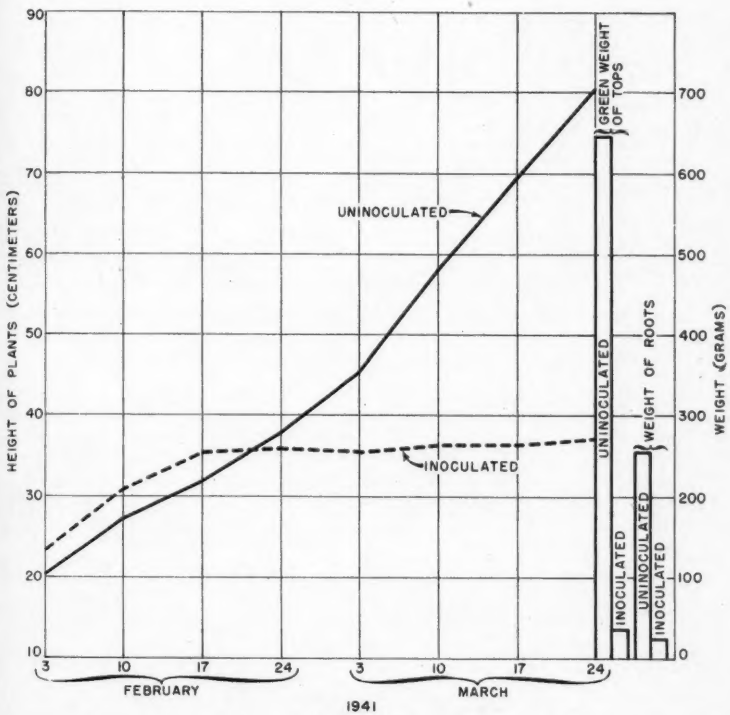

FIGURE 7.—Growth and green weight of tops and weight of roots of plants of dent corn inbred C. I. 1, uninoculated and inoculated with *Pythium arrhenomanes*, Arlington Experiment Farm, 1941.

TABLE 1.—*Weekly increase in height of 12 inbred lines of dent corn not inoculated or inoculated with Pythium arrhenomanes Apr. 1, 1940, and Feb. 3, 1941*

Inbreds	Mean height of plants in—													
	1940: April—					1941								
						February—				March—				
	1	8	15	22	29	3	10	17	24	3	10	17	24
	Cm.	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*
a. L317:													
Not inoculated	21.6	31.8	45.9	57.9	71.5	13.6	20.2	26.7	32.3	39.0	48.3	60.7	72.9
Inoculated	21.9	32.1	44.8	53.3	62.3	15.5	23.8	30.7	35.4	40.1	43.2	48.1	54.4
Difference	−.3	−.3	1.1	4.6	9.2	−1.9	−3.6	−4.0	−3.1	−1.1	5.1	12.6	18.5
Ia. Bl 345:													
Not inoculated	20.5	29.9	41.9	54.2	65.8	14.6	23.0	30.0	34.1	41.4	51.2	61.3	68.3
Inoculated	20.8	30.1	39.4	47.8	54.7	17.6	26.9	32.2	34.2	35.9	37.4	39.0	41.9
Difference	−.3	−.2	2.5	6.4	11.1	−3.0	−3.9	−2.2	−.1	5.5	13.8	22.3	26.4
C. I. 5:													
Not inoculated	28.2	45.8	63.7	81.6	93.4	18.8	30.1	41.7	48.5	59.7	72.3	84.2	96.6
Inoculated	29.1	46.0	58.6	69.1	75.5	20.0	32.8	42.2	45.0	47.3	49.3	51.2	54.6
Difference	−.9	−.2	5.1	12.5	17.9	−1.2	−2.7	−.5	3.5	12.4	23.0	33.0	42.0
Ia. Mc 401:													
Not inoculated	24.9	39.3	54.9	72.8	85.0	15.1	24.7	35.1	40.8	50.3	62.6	74.8	87.0
Inoculated	26.1	40.6	51.8	60.8	68.5	19.4	30.6	40.1	44.2	47.0	51.6	55.3	59.6
Difference	−1.2	−1.3	3.1	12.0	16.5	−4.3	−5.9	−5.0	−3.4	3.3	11.0	19.5	27.4
Ky. 13:													
Not inoculated	30.7	42.0	56.4	71.9	84.8	21.1	31.6	39.4	43.9	49.8	59.6	73.4	86.7
Inoculated	31.1	42.9	50.1	58.8	67.4	25.7	35.8	41.3	44.2	45.9	49.8	52.9	58.8
Difference	−.4	−.9	6.3	13.1	17.4	−4.6	−4.2	−1.9	−.3	3.9	9.8	20.5	27.9
Ill. R4:													
Not inoculated	31.1	49.9	67.4	82.8	91.8	28.0	40.8	52.9	60.3	71.2	81.3	89.4	97.0
Inoculated	29.9	45.3	57.6	65.3	70.5	30.8	43.1	54.2	60.6	65.3	69.2	71.5	72.6
Difference	1.2	4.6	9.8	17.5	21.3	−2.8	−2.3	−1.3	−.3	5.9	12.1	17.9	24.4
Ia. L289:													
Not inoculated	26.3	35.6	54.2	70.1	84.5	19.5	28.7	36.8	42.6	50.3	62.3	74.7	84.5
Inoculated	26.4	37.1	48.7	56.4	64.4	20.6	31.1	36.4	37.6	37.8	40.1	41.8	44.6
Difference	−.1	−1.5	5.5	13.7	20.1	−1.1	−2.4	.4	5.0	12.5	22.2	32.9	39.9
Ill. Hy:													
Not inoculated	27.5	39.0	52.1	65.9	77.3	18.6	28.2	37.1	42.5	49.6	59.7	70.5	80.3
Inoculated	26.4	38.9	45.6	52.8	58.6	21.2	30.7	37.7	41.7	44.6	47.4	49.8	53.4
Difference	1.1	.1	6.5	13.1	18.7	−2.6	−2.5	−.6	.8	5.0	12.3	20.7	26.9
Ind. Tr:													
Not inoculated	22.3	37.0	54.8	73.1	86.3	21.1	32.2	43.9	53.9	67.3	80.4	91.1	98.1
Inoculated	21.0	36.6	44.2	53.0	60.5	24.4	35.4	43.1	48.4	50.6	53.0	54.0	55.0
Difference	1.3	.4	10.6	20.1	25.8	−3.3	−3.2	.8	5.5	16.7	27.4	37.1	43.1
C. I. 4-8:													
Not inoculated	21.4	34.3	47.5	64.3	86.3	23.7	35.9	45.5	52.9	62.7	74.1	85.0	94.1
Inoculated	23.4	36.0	46.1	54.4	60.5	27.5	39.5	49.1	52.6	53.8	55.1	55.8	57.1
Difference	−2.0	−1.7	1.4	9.9	25.8	−3.8	−3.6	−3.6	.3	8.9	19.0	29.2	37.0
C. I. 540:													
Not inoculated	18.7	26.5	37.6	50.4	65.4	18.2	24.7	29.6	33.4	39.7	48.8	59.7	72.9
Inoculated	20.8	31.2	34.9	38.6	42.1	20.0	27.7	31.2	33.6	33.9	35.1	36.0	37.9
Difference	−2.1	−4.7	2.7	11.8	23.3	−1.8	−3.0	−1.6	−.2	5.8	13.7	23.7	35.0
C. I. 1:													
Not inoculated	20.3	30.3	45.0	61.0	76.5	20.6	27.3	31.9	37.9	45.8	58.0	69.7	80.4
Inoculated	22.1	31.3	33.0	38.0	34.6	23.6	30.9	35.1	35.8	35.5	36.2	36.1	37.1
Difference	−1.8	−1.0	12.0	23.0	41.9	−3.0	−3.6	−3.2	2.1	10.3	21.8	33.6	43.3

TABLE 2.—*Results of sand-culture inoculation tests of resistance of 12 inbred lines of dent corn to Pythium arrhenomanes root rot*

Inbred	Mean increase in height of plants in—						Green weight of tops in—				Weight of roots in—			
	1940			1941			1940		1941		1940		1941	
	Total	Difference between control and inoculated	Difference ± controls	Total	Difference between control and inoculated	Difference ± controls	Total	Difference ± controls	Total	Difference ± controls	Total	Difference ± controls	Total	Difference ± controls
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
Ia. L317:	*Cm.*	*Cm.*[1]	*Percent*	*Cm.*	*Cm.*[2]	*Percent*	*Gm.*	*Percent*	*Gm.*	*Percent*	*Gm.*	*Percent*	*Gm.*	*Percent*
Not inoculated	49.9	−9.5	−19.0	59.3	−20.4	−34.4	343.9	−11.1	494.0	−58.1	271.0	−24.0	198.0	−58.6
Inoculated	40.4			38.9			305.8		207.0		206.0		82.0	
Ia. Bl 345:														
Not inoculated	45.3	−11.4	−25.2	53.7	−29.4	−54.7	482.4	−44.2	500.0	−77.7	220.0	−32.7	157.5	−84.8
Inoculated	33.9			24.3			269.3		111.5		148.1		24.0	
C. I. 5:														
Not inoculated	65.2	−18.8	−28.8	77.8	−43.2	−55.5	641.2	−51.6	848.0	−79.0	334.5	−35.5	243.0	−71.2
Inoculated	46.4			34.6			310.1		178.0		215.6		70.0	
Ia. Mc 401:														
Not inoculated	60.1	−17.7	−29.5	71.9	−31.7	−44.1	500.0	−44.0	537.0	−68.1	332.5	−42.9	200.0	−70.0
Inoculated	42.4			40.2			280.0		171.5		190.0		60.0	
Ky. 13:														
Not inoculated	54.1	−17.8	−32.9	65.6	−32.5	−49.5	480.6	−51.5	562.5	−67.4	297.7	−35.8	284.0	−74.1
Inoculated	36.3			33.1			233.3		183.5		191.1		73.5	
Ill. R 4:														
Not inoculated	60.7	−20.1	−33.1	69.0	−27.2	−39.4	625.1	−63.2	901.0	−61.1	321.1	−62.6	411.0	−68.0
Inoculated	40.6			41.8			230.0		350.2		120.0		131.5	
Ia. L289:														
Not inoculated	58.2	−20.2	−34.7	65.0	−41.0	−63.1	488.8	−57.9	501.2	−89.4	271.1	−54.7	172.0	−85.5
Inoculated	38.0			24.0			205.7		53.2		122.8		25.0	
Ill. Hy:														
Not inoculated	49.8	−17.6	−35.3	61.7	−29.5	−47.8	444.1	−56.2	479.1	−70.1	272.8	−54.4	122.5	−49.4
Inoculated	32.2			32.2			194.6		143.2		124.5		62.0	
Ind. Tr:														
Not inoculated	64.0	−24.5	−38.3	77.0	−46.4	−60.3	463.5	−68.0	885.2	−86.0	262.2	−60.2	470.0	−88.0
Inoculated	39.5			30.6			148.5		124.0		104.3		56.2	
C. I. 4–8:														
Not inoculated	64.9	−27.8	−42.8	70.4	−40.8	−58.0	448.0	−65.4	757.0	−82.2	245.0	−60.4	284.3	−81.9
Inoculated	37.1			29.6			155.0		135.0		96.9		51.5	
C. I. 540:														
Not inoculated	46.7	−25.4	−54.4	54.7	−36.8	−67.3	292.7	−81.5	362.7	−91.1	189.0	−73.0	229.5	−87.8
Inoculated	21.3			17.9			54.2		32.3		51.0		28.0	
C. I. 1:														
Not inoculated	56.2	−43.7	−77.8	59.8	−46.3	−77.4	510.0	−96.5	646.0	−94.5	284.5	−92.8	254.0	−91.3
Inoculated	12.5			13.5			17.9		35.5		20.6		22.0	

[1] Difference between differences required for significance, 16.3 cm.

[2] Difference between differences required for significance, 9.5 cm.

Differences in growth of tops between inoculated and control plants of individual replicates were analyzed statistically[9] by the analysis of variance method, and the required difference for significance between mean differences was calculated for each of the two experiments. In 1940 this difference was $1.971\sqrt{\frac{2\times2\times171.51}{10}}=16.32$ cm.; and in 1941, $1.971\sqrt{\frac{2\times2\times57.50}{10}}=9.45$ cm.

The difference between Ia. L317, the most resistant inbred, and C. I. 1 was significant in each year. In 1941, in the longer test, there

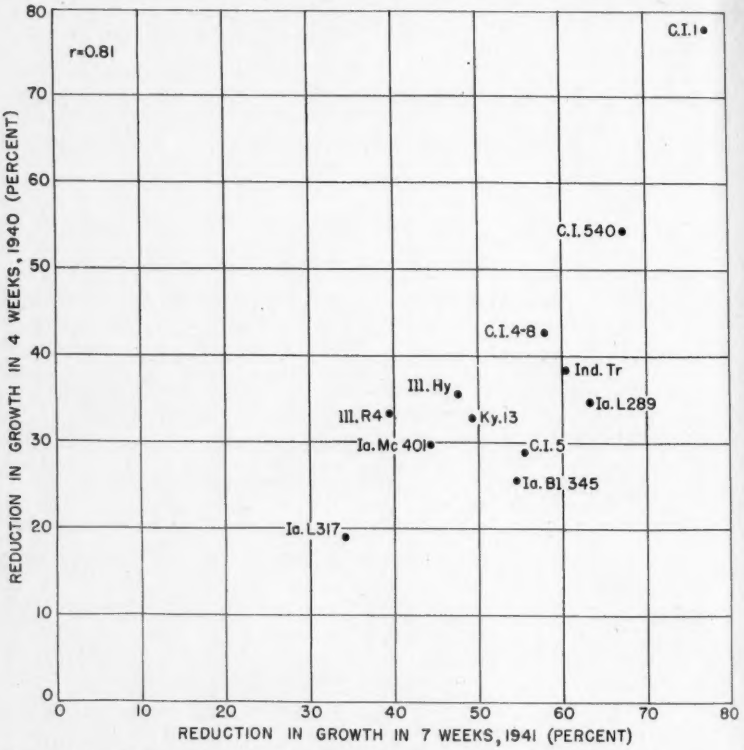

FIGURE 8.—Scatter diagram of percentage reduction in growth of dent corn inbreds inoculated with *Pythium arrhenomanes*, 1940 and 1941.

were significant differences between Ia. L317 and all other inbreds except Ia. Bl. 345, Ill. R4, and Ill. Hy.

In both years, inbred Ia. L317 was more resistant to root rot than any other inbred and C. I. 1 was more susceptible than any other. Inbred Ia. L317 is one of the most widely used inbreds in the development of hybrids in the Corn Belt. Although the results are not iden-

[9] The statistical work was done by O. E. Rauchschwalbe, of the Division of Cereal Crops and Diseases, Bureau of Plant Industry.

tical for the two tests, this is at least partly due to differences in environmental conditions difficult to control. According to other workers,[10] root rot due to *Pythium arrhenomanes* develops most abundantly under cool moist conditions. In the second experiment, the steam pipes undoubtedly had an influence on the inoculated plants of Ill. R4 and possibly other inbreds that were next to the pipes.

Percentage reductions in growth of tops (columns 3 and 6) for 1940 and 1941 are compared in a scatter diagram (fig. 8). Variability about the line of regression is an indication of the interaction between environment and strain in the two tests.

It should be noted that these are the results of inoculations with one strain of *Pythium arrhenomanes* isolated from root rot in dent corn growing under field conditions in one section of the Corn Belt. It is possible that there may be other strains of this fungus in other localities that may be more or less virulent than the strain used. Rands and Dopp[11] already have found that there may be wide differences in virulence in isolates of *P. arrhenomanes* from sugarcane in the same field and that populations may vary from season to season. It is possible that this may be true also for the fungus on corn.

SUMMARY

Twelve inbred lines of dent corn were tested for susceptibility to root rot by inoculation with *Pythium arrhenomanes*. The plants were grown in sand, watered with nutrient solution, and inoculated by adding agar cultures of the fungus to the sand after the plants were well established. Weekly measurements of growth of inoculated and uninoculated plants and weights of tops and roots showed that some inbreds were susceptible to root rot, some were resistant, and others were intermediate in reaction. Inbred Ia. L317 was the most resistant and inbred C. I. 1 the most susceptible. The fungus interfered to some extent with the growth of all the inbreds by destroying the fine feeding roots.

[10] See footnote 5.
[11] See footnote 5.

RESERVE FOODS IN THE ROOTS OF WHITEWEED (CARDARIA DRABA VAR. REPENS)[1]

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INTRODUCTION

The food reserves in the roots of perennial weeds have been studied by a number of investigators who have assigned important roles to various carbohydrate fractions in attempts to determine the most effective methods of weed control. Bakke, Gaessler, and Loomis [3] found that sucrose and a dextrinlike compound or group of compounds are the characteristic reserves in bindweed. Barr [4] found that the reserves in the bindweed of his experiments consisted largely of sucrose and a polysaccharide fraction extracted with taka-diastase and commonly designated as starch. He did not, however, attempt to determine dextrin and starch separately.

The literature on the organic reserves in the roots of whiteweed is very limited.

Investigations of the reserve food in the roots of weeds were started at the Colorado Agricultural Experiment Station in 1935. The experiments discussed in this paper relate to the carbohydrate and nitrogen content of whiteweed roots as affected by various cultural practices and chemical treatments. All the experiments except as otherwise noted were conducted on land subject to irrigation but not irrigated during the course of the study.

MATERIALS AND METHODS

The material used for the experiments was the roots of whiteweed *Cardaria draba* (L.) Desv. var. *repens* (Schrenk) O. E. Schulz). Four separate types of collections were made to study the effects of cultivation and application of sodium chlorate on the root reserves:

(1) Root samples collected at biweekly intervals from April to December. Two series of plots were sampled, one in which the plants were undisturbed throughout the season, and the other in which the plants were clean-cultivated at 2-week intervals from April to October.

(2) Root samples collected at 4-day intervals for a period of 24 days (a) after a single cultivation in the spring, and (b) after small-grain harvest but without cultivation.

(3) Root samples collected from cultivated and undisturbed plots treated on various dates (tables 6 and 7) with dry sodium chlorate

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[2] Thanks are due Bruce J. Thornton, associate professor of botany, from whose experimental plots the samples for this investigation were taken, and to Dr. L. W. Durrell, head of the Department of Botany and Plant Pathology, for helpful advice during the progress of this investigation.

[3] BAKKE, A. L., GAESSLER, W. G., and LOOMIS, W. E. RELATION OF ROOT RESERVES TO CONTROL OF EUROPEAN BINDWEED, CONVOLVULUS ARVENSIS L. Iowa Agr. Expt. Sta. Res. Bul. 254, pp. 113-144. 1939.

[4] BARR, C. GUINN. PRELIMINARY STUDIES ON THE CARBOHYDRATES IN THE ROOTS OF BINDWEED. Amer. Soc. Agron. Jour. 28: 787-798, illus. 1936.

at the rate of 3 pounds per square rod. Samples were taken at the time of treatment; viz, June 1, June 30, August 2, September 1, September 17, and September 30, and also 1 month after treatment. Checks were run on untreated and uncultivated plots.

(4) Root samples collected at the end of the growing season, about October 1, from plots (a) undisturbed; (b) cultivated weekly, April to October; and (c) cultivated biweekly, April to October.

COLLECTING AND ANALYZING SAMPLES

The method used in collecting the root samples, described in a previous report,[5] consisted in sifting the soil containing whiteweed roots and placing the roots with some soil in quart mason fruit jars for transport to the laboratory. A post-hole digger which made a hole 6 inches in diameter was used in digging the roots. By making four adjacent holes in the pattern of a square, a hole was produced 1 foot square and as deep as required. For the work on whiteweed, root samples were taken from both the first- and second-foot levels. Live roots only were taken, all dead and decaying portions such as were found in the cultivated plots being discarded. A cubic foot of soil was taken from each of five different locations in the plot to make up a standard composite field sample.

The roots were taken to the laboratory as soon as possible after digging, the soil and sand were removed, and the roots were washed with cold water. The excess water was removed by blotting with cheesecloth. Duplicate 50-gm. samples of the roots were weighed to ± 0.05 gm. on a torsion balance. These were cut into pint mason fruit jars containing 200 ml. of boiling 95-percent alcohol, sealed, and allowed to simmer in a boiling water bath for 45 to 60 minutes. The samples were then stored until they could be conveniently extracted and analyzed.

The preserved root material was extracted by decantation with 80-percent boiling alcohol until reducing substances had been removed from the sample as determined by tests. From 10 to 14 extractions were required. The extract from each sample was collected in a volumetric flask and the extracting liquor made to volume after completion of the extraction. Two hundred milliliter portions of this liquor were used for the sugar determinations. The alcohol was removed by evaporation and the resulting water solution was cleared with neutral lead acetate. Reducing substances were determined, after invertase digestion, by reduction of alkaline potassium ferricyanide and titration of the reduced iron with standard ceric sulphate solution.

It should be pointed out that considerable trouble was encountered in making sugar determinations by the Munson-Walker method. During the heating of the water solution of sugars with Fehling's solution, a colloidal mass of reduced copper together with other interfering substances was produced which caused great difficulty in filtering. This precipitate was difficult to break up on the asbestos mat in the Gooch Crucible, and it was not entirely soluble in the ferric ammonium sulfate. Titration of the reduced iron with potassium permanganate gave results which disagreed as much as 100 percent when duplicate aliquots were run from the same sample. The source of error was shown to be in the precipitation of the copper, and in the

[5] BARR, C. G. ORGANIC RESERVES IN THE ROOTS OF BINDWEED. Jour. Agr. Res. 60: 391, 413, illus. 1940.

fact that the end point was unstable in the permanganate titration. Tests showed that both clearing and deleading were complete. Whether the difficulty was due to salts contained by the roots of whiteweed, extractable with boiling 80-percent alcohol, or to certain complex carbohydrate compounds peculiar to whiteweed or to both is not known. Osazone reactions after hydrolysis with dilute hydrochloric acid or invertase yielded a mixture of crystals resembling glucosazones, maltosazones, and other unidentified crystals which suggested the presence of trisaccharides.

Ceric sulfate was found to be suitable in the analysis of carbohydrates in the roots of bindweed and whiteweed,[6] hence, ceric sulfate was used throughout this experiment in estimating the quantities of reducing substances.

The residue, after the removal of the soluble carbohydrates, was dried to constant weight at 100° C., ground to suitable fineness, and analyzed for starch and acid-hydrolyzable materials separately.

For the starch determinations, 1-gm. samples of the residue were gelatinized and digested with undiluted taka-diastase until negative iodine tests for starch were obtained. The digest was then filtered and washed, the filtrate was cleared with neutral lead acetate, and the glucose equivalent after hydrolysis was determined on aliquots. It has been pointed out in a previous paper [5] that in the determination of starch by this method, small amounts of other substances that yield reducing substances upon hydrolysis may be brought into solution by the gelatinizing process and taka-diastase digestion. The technique, serves, however, to give an adequate estimation of the important reserve polysaccharides.

FORM OF FOOD RESERVES IN THE ROOTS OF WHITEWEED

Important food reserves in whiteweed occur in the form of sugar and starch. Only small quantities of reducing sugars were found, amounting to less than 1.50 percent in August and showing only moderate fluctuation. Determinations for reducing sugars were, therefore, not made on all the samples. Although other carbohydrate fractions, such as the dextrins and a group of compounds extracted with hot dilute mineral acids, do occur, the writer's experiments have shown that they probably play a less important role than the sugars and starch.

Whiteweed roots are unusually high in starch content and a cross section of a root appears not unlike the cross section of a potato. At the peak of accumulation the tissue is gorged with starch and an intense blue-black color is produced with iodine in potassium iodide solution over the entire section, indicating the vast amount of starch present. The moisture content of whiteweed root tissue varies from 70 to 90 percent, depending upon the environmental conditions under which the plant grows.

Results for the carbohydrate analyses were calculated as: (1) percentage of fresh weight, (2) percentage of dry weight, and (3) percentage of residual dry weight; that is, calculations were made on the dry weight of the tissue after the soluble carbohydrates and the polysaccharides were removed. The residual dry-weight calculations were difficult to interpret and their meaning was of little value from the standpoint of a cultivation control program, and the dry-weight

[5] BARR, C. G. ORGANIC RESERVES IN THE ROOTS OF BINDWEED. Jour. Agr. Res. 63: 391, 413, illus. 1940.
[6] BARR, C. G. APPLICATION OF THE CERIC SULPHATE METHOD IN THE ANALYSIS OF CARBOHYDRATES IN THE ROOTS OF LEPIDIUM AND CONVOLVULUS. Plant Physiol. 14: 285-296, illus. 1939.

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calculations were so high and variable that they seemed worthless. The readily available carbohydrates are expressed in the tables, however, as percentage of both the fresh weight and the dry weight for comparison.

The value of the dry-weight data may be estimated from a study of table 1. Samples for the second-foot level on September 30 contained 2.04 percent total sugar and 21.14 percent starch, amounting to 23.18 percent readily available carbohydrates. It has been shown [6] that carbohydrates determined by the method used in this study are 1 to 5 percent higher than by the official Munson-Walker method. The percentages obtained here, therefore, are reasonably accurate, but assuming the actual readily available carbohydrate content to be about 20 percent, 20 gm. of every 100 gm. of fresh plant material would represent respirable material. The particular sample under consideration contained 72 percent of moisture, or 28 gm. of dry plant material. The quantity of readily available carbohydrates would, therefore, be over 80 percent on the dry-weight basis and would vary from 77 percent to 89 percent with a change of sample moisture content of ±2 percent. If, however, the data are calculated on the fresh-weight basis, a variation of ±2 percent in moisture content of the sample would result in a change of readily available carbohydrates from 21.50 percent to 24.81 percent. It seems desirable, therefore, to base interpretations on fresh weight.

TABLE 1.—*Seasonal trends in the carbohydrate content (percent) of whiteweed roots in the first- and second-foot levels of undisturbed and cultivated plants, 1936*

[The two sets of data for each sampling date are for the first- and second-foot levels, respectively]

Date of sampling	Undisturbed plants						Cultivated plants					
	Reducing sugars	Total sugars	Starch	Acid hydrolyzable substances	Readily available carbohydrates on bases of—		Reducing sugars	Total sugars	Starch	Acid hydrolyzable substances	Readily available carbohydrates on basis of—	
					Fresh weight	Dry weight					Fresh weight	Dry weight
Apr. 25	0.73	1.50	2.69	2.35	4.19	33.6						
	.63	2.82	1.64	2.13	4.46	35.06						
May 9	.56	1.72	2.07	3.92	3.79	33.33	0.67	1.38	1.65	2.71	3.03	22.80
	.67	2.26	2.27	3.23	4.54	32.70	.66	2.79	3.96	1.72	6.75	61.38
May 25	.78	2.15	7.41	3.52	9.56	48.72	.62	1.46	2.74	2.51	4.20	35.23
	.66	2.88	6.41	3.07	9.29	58.07	.66	2.68	3.81	2.27	6.49	59.55
June 8	.70	2.77	12.20	2.81	14.97	54.67	.50	1.00	4.39	3.43	5.39	47.11
	.80	3.95	13.80	3.19	17.75	75.77	.60	1.60	3.78	2.43	5.38	55.57
June 22	.81	1.91	15.77	5.67	17.68	59.36	.44	.92	1.59	3.27	2.51	20.52
	.79	3.02	15.94	6.44	18.96	83.23	.18	.82	3.05	2.35	3.87	39.38
July 6	1.24	3.78	18.36	8.08	22.14	66.16	.55	1.42	3.03	2.75	4.45	42.20
	1.02	4.16	19.45	6.71	23.61	92.47	.56	1.85	3.53	2.14	5.38	54.69
July 21	1.16	2.96	21.88	6.61	24.84	71.50	.71	2.11	4.54	2.59	6.65	53.20
	.93	3.86	20.50	4.91	24.36	95.52	.68	2.12	3.81	3.03	5.93	48.52
Aug. 2	1.41	2.77	21.24	4.74	24.01	68.57	.76	2.52	3.76	3.28	6.28	62.50
	1.28	2.88	22.43	4.33	25.31	71.70	.67	3.17	3.40	3.48	6.57	65.50
Aug. 18	1.32	2.20	16.80	5.25	19.00	58.82						
	1.33	2.99	19.68	3.84	22.67	74.53						
Sept. 1	1.16	1.98	17.04	4.96	19.02	54.81						
	1.04	2.96	20.19	3.18	23.15	76.55						
Sept. 13	1.06	2.16	15.38	5.05	17.54	55.15						
	.93	2.24	21.27	3.13	23.51	79.93						
Sept. 30		2.51	14.77	4.86	17.28	64.14						
		2.04	21.14	3.09	23.18	82.78						
Oct. 16		3.49	14.73	4.67	18.22	64.15						
		3.10	18.36	3.33	21.46	82.54						
Oct. 29		5.46	15.08	4.89	20.54	72.83						
		4.36	19.36	3.32	23.72	88.92						
Dec. 3		7.44	9.00	4.66	16.44	72.10						
		6.65	12.77	3.41	19.42	89.90						

[6] BARR, C. G. APPLICATION OF THE CERIC SULPHATE METHOD IN THE ANALYSIS OF CARBOHYDRATES IN THE ROOTS OF LEPIDIUM AND CONVOLVULUS. Plant Physiol. 14: 285–296, illus. 1939.

TREND OF ROOT RESERVES DURING THE SEASON

Total sugars and starch show marked accumulation in the roots of undisturbed whiteweed plants from April to early summer. Roots from the second-foot level contained uniformly more total sugars than those from the first-foot level until about the middle of September, when the percentages were reversed (table 1, fig. 1). There was a gradual accumulation of sugars from April 25 to July 6, 1936, when a maximum of about 4 percent was reached. The initial accumulation was followed by a steady decrease until about the middle of September,

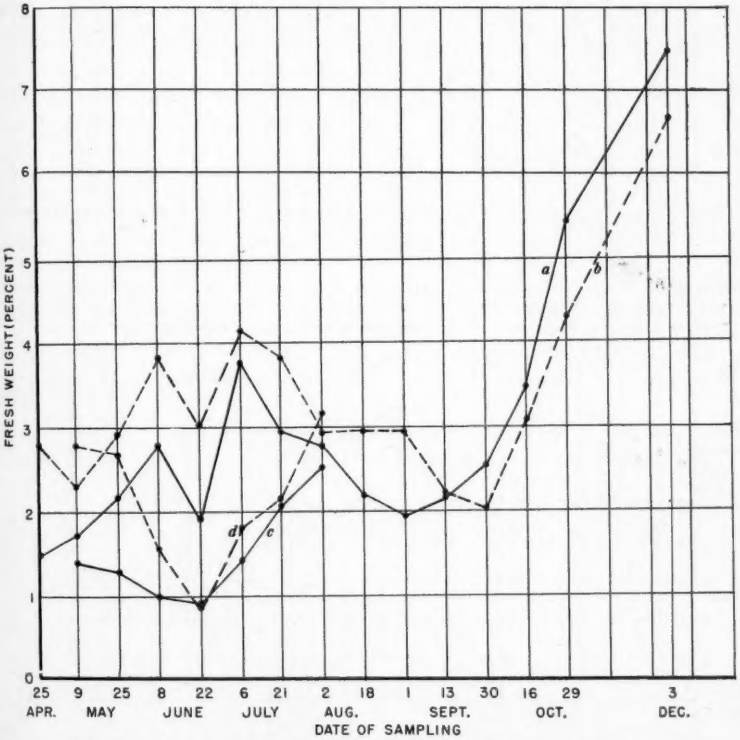

FIGURE 1.—Total sugar content of whiteweed roots when undisturbed and when cultivated at 2-week intervals, 1936: *a*, First foot, undisturbed; *b*, second foot, undisturbed; *c*, first foot, cultivated; *d*, second foot, cultivated.

after which the sugar content increased rapidly, reaching 6 or 7 percent by December 3 (fig. 1). The rapid increase in total sugar content after October 1 is interpreted as the result of the shift from polysaccharides to sugars that commonly occurs in plants as cold weather approaches. Evidence supporting this interpretation is the simultaneous reduction in the percentage of starch as the sugar content increased (compare figs. 1 and 2). The same observation has been made at this station in work on reserves in bindweed. A noteworthy point is the lag in the

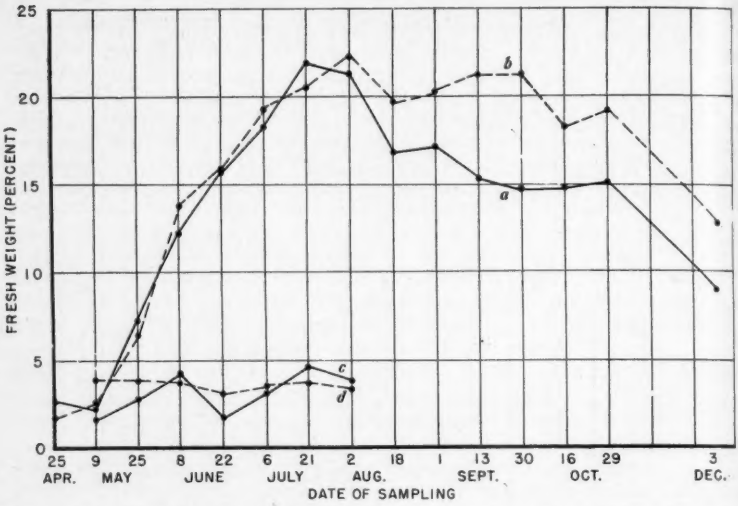

FIGURE 2.—Starch content of whiteweed roots when undisturbed and when cultivated at 2-week intervals, 1936: *a*, First foot, undisturbed; *b*, second foot, undisturbed; *c*, first foot, cultivated; *d*, second foot, cultivated.

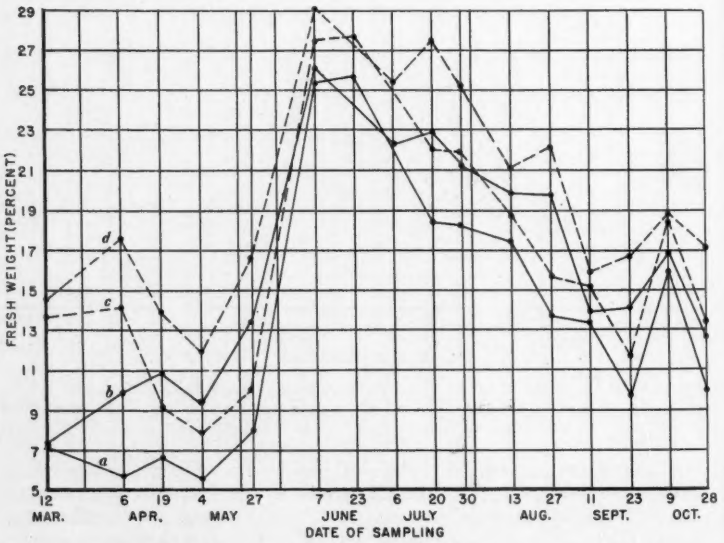

FIGURE 3.—Starch and readily available carbohydrate content of whiteweed roots undisturbed, 1937: *a*, Starch, first foot; *b*, starch, second foot; *c*, readily available carbohydrates, first foot; *d*, readily available carbohydrates, second foot.

maximum percentage of starch which occurred about 1 month later than the initial maximum total sugar content. An unexpected high value of over 20 percent (fresh-weight basis) of starch was found in the roots of undisturbed plants.

Plants that were clean-cultivated at 2-week intervals throughout the season failed to show a total sugar content greater than 3.17 percent, and cultivation held the starch to about 4.54 percent. Plants on the cultivated areas were rapidly disappearing by the last of June, and when samples were collected on July 6 considerable difficulty was encountered in finding sufficient roots to preserve for analysis. Many dead and decaying roots were found on this and the next two sampling dates, and no samples could be collected from the cultivated area after August 2. During the summer of 1937 only a very few scattered plants appeared on the clean-cultivated areas. Under the conditions of the experiments, therefore, 96 to 98 percent eradication was obtained by one season of clean cultivation.

It should be pointed out also that the infestation of whiteweed in the Fort Collins area was limited; plots were not available in 1937 for extended systematic cultivation studies and for this reason the data for 1937 are meager. Samples were collected, however, which yielded information on the seasonal trend of root reserves in undisturbed plants (table 2 and fig. 3).

TABLE 2.—*Seasonal trends in the carbohydrate and nitrogen content (percent) of whiteweed roots in the first- and second-foot levels of undisturbed plants, 1937*

[The two sets of data for each sampling date are for the first- and second-foot levels, respectively]

Date of sampling	Total sugars	Starch	Acid-hydrolyzable substances	Readily available carbohydrates on basis of—		Colloidal nitrogen	Soluble nitrogen
				Fresh weight	Dry weight		
Mar. 12	6.44	7.21	4.19	13.65	61.22	0.429	0.293
	7.27	7.31	2.28	14.58	85.23	.176	.250
Apr. 6	8.55	5.71	3.92	14.26	69.29	.414	.278
	7.65	9.96	3.53	17.61		.192	.181
Apr. 19	2.35	6.77	4.03	9.12	44.75	.399	.234
	2.99	10.90	2.11	13.89	71.62	.181	.150
May 4	2.36	5.61	3.74	7.97	38.08	.260	.156
	2.36	9.52	2.65	11.88	61.36	.138	.107
May 27	2.13	8.04	5.09	10.17	36.79	.239	.086
	3.12	13.47	4.53	16.59	65.40	.173	.080
June 7	2.28	25.31	5.40	27.59	49.96	.254	.087
	3.08	26.03	3.59	29.11		.174	.100
June 23	2.08	25.67	5.66	27.75	74.14	.384	.140
	3.80		3.58			.296	.137
July 6	2.13					.426	.168
	3.07	22.33	1.90	25.40	71.10	.279	.145
July 20	3.70	18.40	3.21	22.10	56.46	.468	.216
	4.56	22.94	4.64	27.50	69.57	.285	.182
July 30	3.70	18.28	2.60	21.98	57.18	.485	.228
	3.97	21.24	2.31	25.21	63.93	.365	.199
Aug. 13	1.26	17.42	7.67	18.68	50.29	.505	.195
	1.16	19.86	5.91	21.02	58.64	.365	.164
Aug. 27	1.91	13.70	7.40	15.61	44.19	.428	.204
	2.31	19.79	5.31	22.10	63.43	.554	.222
Sept. 11	1.77	13.38	7.80	15.15	45.09	.284	.221
	2.02	13.89	9.98	15.91	46.64	.408	.162
Sept. 23	1.85	9.76	4.24	11.61	39.48	.320	.166
	2.44	14.18	2.35	16.62	57.96	.221	.166
Oct. 9	2.43	16.06	4.79	18.49	56.27	.539	.222
	1.90	16.91	2.46	18.81	55.33	.364	.193
Oct. 28	3.43	9.91	4.25	13.34	42.13	.486	.262
	4.42	12.66	2.35	17.08	53.30	.338	.243

The observed increase in the sugar content of the roots of cultivated plants after June 22, 1936, suggests that translocation of soluble carbohydrates has taken place from lower to upper roots. The soluble carbohydrates in the lower roots would presumably be derived from complex carbohydrate reserves. It suggests further that the continual regeneration of new-shoot growth brought about by the frequent cultivations stimulated enzymatic activity which resulted in higher soluble-carbohydrate content at the expense of complex reserves in the deeper roots. Whiteweed root samples taken to a depth of 3 feet in 1935 showed progressive increases in total sugars and starch with increasing depths from which the roots were collected.

The reducing sugars and acid-hydrolyzable substances showed no important variations in either undisturbed or cultivated plants.

Owing to lack of material, it was not possible to make nitrogen determinations on the samples collected in 1936. Analyses were made,

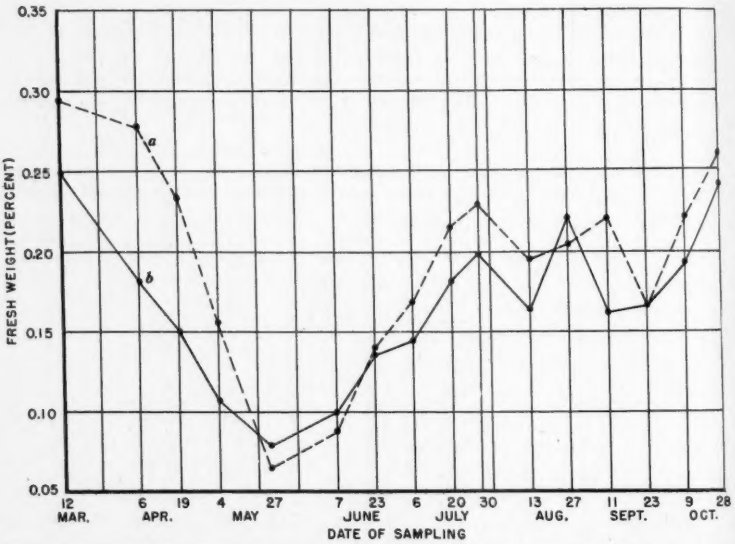

FIGURE 4.—Soluble nitrogen content of whiteweed roots when undisturbed, 1937: *a*, First foot; *b*, second foot.

however, for soluble and residual nitrogen in the roots collected in 1937. The data are given in table 2 and shown graphically in figures 4 and 5.

The marked decrease in soluble nitrogen from March until the latter part of May suggests the rapid utilization of that fraction in vegetative growth. Field notes taken during this time show that the plants exhibited considerable vegetative growth until the end of May when flowering was initiated. Mature seeds were observed by June 23 and the plants appeared to be going into a dormant condition. From June 23 until August 13 there was a period of vegetative inactivity and the soluble nitrogen content increased from about 0.07 percent from May 27 to over 0.20 percent by August 27.

A noteworthy point also is the relation between soluble nitrogen and carbohydrates during the period of vegetative growth in April and May. The elaboration of carbohydrates was apparently not sufficiently rapid to keep pace with the rate of their utilization in the formation of new protoplasts. The roots, being reserve sources of supply for the materials necessary for growth, showed a reduction of about 44 percent in carbohydrate content during the period from April 6 to May 4. The carbohydrates and soluble nitrogen each showed distinct accumulation after flowering, but the carbohydrates increased at a considerably more rapid rate than the nitrogen.

The fluctuation in the colloidal nitrogen content from March 12 to August 13 closely resembled that of the soluble nitrogen during the same period. This was especially true of the roots from the first foot of soil. Both the soluble and the residual nitrogen showed such peculiar

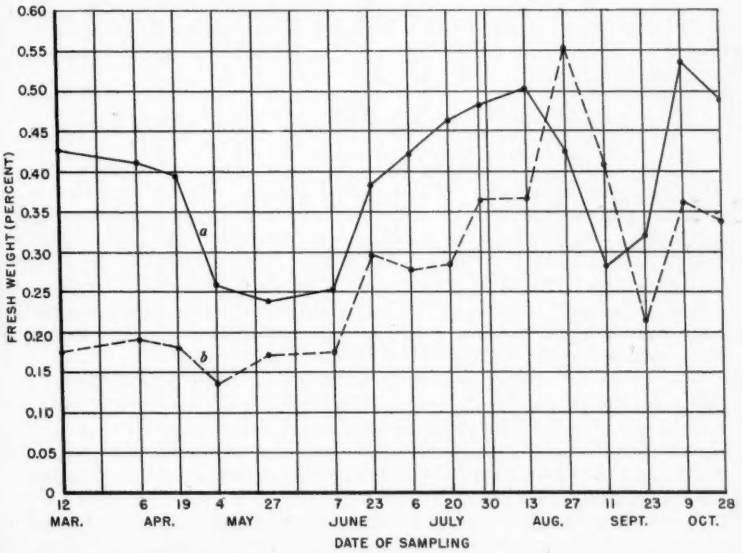

FIGURE 5.—Colloidal nitrogen content of whiteweed roots when undisturbed, 1937: *a*, First foot; *b*, second foot.

fluctuations after August 13 that it is difficult to attach any meaning to the variations.

A series of collections at 4-day intervals was started on July 21 after the harvest of wheat growing on whiteweed infested land. During the period from July 21 to August 14 the weather was uniformly cool; field notes show that the daytime temperatures were 70° to 76° F. No rain was recorded for this period and the plot was not cultivated and received no irrigation after the wheat harvest. Sampling on the area was continued until about the middle of August, but no important changes occurred in the carbohydrates under the conditions of the experiment. There was, however, an increase in the carbohydrate content as compared with that in the early-season collection. The data are given in table 3.

TABLE 3.—*Seasonal trends in the carbohydrate content (percent) of the roots of noncultivated whiteweed after wheat harvest, first- and second-foot levels, 1936*

[The two sets of data for each sampling date are for the first- and second-foot levels, respectively]

Date of sampling	Reducing sugars	Total sugars	Starch	Acid-hydrolyzable substances	Readily available carbohydrates on basis of—	
					Fresh weight	Dry weight
July 21	1.16	2.74	21.88	6.61	24.62	71.50
	.93	3.94	20.53	4.91	24.47	95.52
July 25	1.40	2.97	23.06	4.94	26.03	69.38
	1.15	3.31	27.45	3.90	30.76	92.40
July 29	1.34	2.58	21.36	5.64	23.94	68.91
	1.30	3.49	24.55	3.89	28.04	95.05
Aug. 2	1.41	2.77	21.24	4.74	24.01	68.57
	1.28	2.88	22.43	4.33	25.31	71.70
Aug. 6	1.16	2.37	18.09	5.41	20.46	62.18
	.85	3.47	17.75	3.31	21.22	79.77
Aug. 10	1.34	2.32	18.85	5.26	21.17	61.87
	1.03	2.94	20.80	3.40	23.74	78.87
Aug. 14	1.29	2.34	20.18	4.89	22.52	62.43
	1.13	3.33	20.19	4.46	23.52	78.85

TREND OF ROOT RESERVES AFTER CULTIVATION

An area uniformly infested with whiteweed was cultivated on May 1, 1936, but not thereafter. Root samples were collected at 4-day intervals for a period of 24 days after the cultivation. Samples were taken at the same time from an adjacent control plot that had not been cultivated, but was otherwise similar. The plants on these plots emerged about April 15. On May 9 the undisturbed plants were 6 to 10 inches high and were 90 percent in full bloom; the undisturbed plants were in full bloom on May 16. The plants on the cultivated area emerged between May 9 and May 15.

The trend of the starch and readily available carbohydrates [7] in the roots from the top 2 feet of soil, undisturbed and cultivated, is shown in table 4. The data for only the first-foot level are plotted in figure 6 since the fluctuations in the sugar and starch content of the roots from the first foot of soil seemed to show the general trend for the second foot also.

Only a moderate increase in the carbohydrate content occurred in the roots of either the undisturbed or the cultivated plants during the first 12 to 16 days after cultivation. Twelve days after the beginning of the experiment there was a surprisingly rapid increase in the readily available carbohydrate content of the roots of the undisturbed plants. On May 25 the readily available carbohydrates were nearly 300 percent of their value on May 12. The low point in the carbohydrates for the cultivated plants was 4 days later than for the undisturbed plants, and although there was a distinct accumulation after 16 days, the readily available carbohydrate content on May 25 was about 176 percent of its value on May 16. Accumulation of reserves was delayed apparently by cultivation, but in spite of cultivation the plants showed a marked increase in root reserves after 16 days.

The experiment was repeated in 1937. The plot was cultivated on May 8 and again on May 17, when the first root samples were col-

[7] The term "readily available carbohydrates" is used in this paper to express the sum of the total sugar and starch, commonly assumed to be readily available reserve materials.

lected. Vegetative growth was limited by the low soil-moisture content but a few plants were emerging on May 22. On May 31 there was 0.75 inch of rain and during the first 6 days of June there was a total of 1 inch of rain. The results of the study in 1937 are similar to those obtained in 1936, as a comparison of the data in tables 4 and 5 will show. In the 1937 experiment the accumulation started about 10 days after cultivation and the total carbohydrate content was increasing rapidly at the end of the experiment on June 7.

While it may not seem necessary to cultivate oftener than at inter-

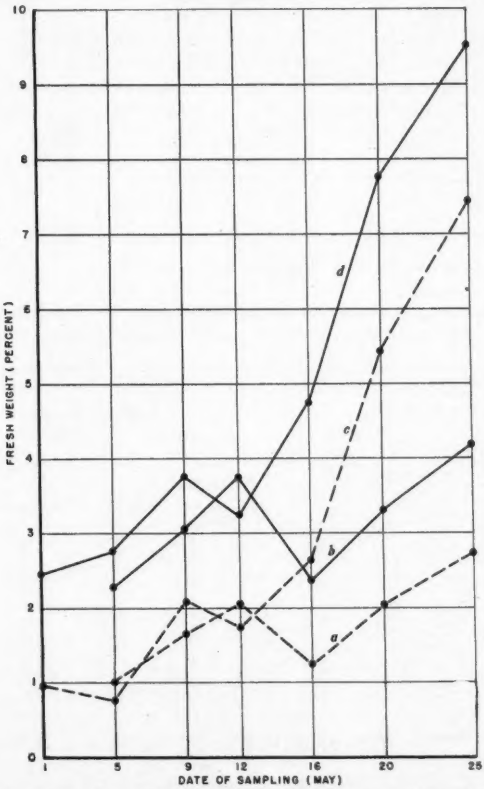

FIGURE 6.—Carbohydrate content of whiteweed roots first-foot level, after cultivation. Sampled at time of cultivation and at approximately 4-day intervals for a period of 24 days; *a*, Starch, cultivated; *b*, readily available carbohydrates, cultivated; *c*, starch undisturbed; *d*, readily available carbohydrates, undisturbed.

vals of 16 days, the data suggest that any delay beyond 16 days would permit rapid accumulation of reserves. It is likely that the interval might be lengthened if a second or even a third cultivation should be made coincident with the start of reserve-food accumulation as indicated by the analysis of roots.

TABLE 4.—*Seasonal trends in the carbohydrate content (percent) of whiteweed roots after cultivation in the first- and second-foot levels, 1936*

[The two sets of data for each sampling date are for the first- and second-foot levels, respectively]

Date of sampling	Uncultivated					Cultivated May 1				
	Total sugars	Starch	Acid-hydrolyzable substances	Readily available carbohydrates on the basis of—		Total sugars	Starch	Acid-hydrolyzable substances	Readily available carbohydrates on the basis of—	
				Fresh weight	Dry weight				Fresh weight	Dry weight
May 1	1.50	0.97	0.74	2.47	18.98					
	2.49	.83	2.46	3.32	27.39					
May 5	2.02	.76	2.70	2.78	17.13	1.21	1.00	3.06	2.21	14.74
						2.62	3.43	2.44	6.05	43.32
May 9	1.72	2.07	3.92	3.79	23.92	1.38	1.65	2.71	3.03	22.80
	2.26	2.27	3.23	4.53	32.70	2.79	3.96	1.72	6.75	61.38
May 12	1.52	1.74	3.15	3.26	22.23	1.72	2.02	2.38	3.74	29.40
	2.22	2.36	2.75	4.58	32.52	2.43	2.22	2.07	4.65	40.34
May 16	2.06	2.65	3.11	4.71	32.33	1.17	1.21	2.51	2.38	18.45
	2.45	3.70	2.10	6.15	47.30	1.74	2.00	2.19	3.74	32.81
May 20	2.24	5.46	4.70	7.70	37.48	1.25	2.05	3.56	3.30	26.05
	2.86	6.23	3.88	9.09	54.96	2.14	3.22	3.07	5.36	44.46
May 25	2.15	7.41	3.82	9.56	48.72	1.46	2.74	2.51	4.20	48.72
	2.88	6.41	3.07	9.29	58.07	2.71	3.82	2.27	6.53	59.55

TABLE 5.—*Seasonal trends in the carbohydrate content (percent) of whiteweed roots after cultivation, in the first- and second-foot levels, 1937*

[The two sets of data for each sampling date are for the first- and second-foot levels, respectively]

Date of sampling	Total sugars	Starch	Acid-hydrolyzable substances	Readily available carbohydrates on basis of—		Colloidal nitrogen	Soluble nitrogen
				Fresh weight	Dry weight		
May 17	1.35	7.71	3.76	9.06	43.18	0.220	0.171
		11.20	3.06			.144	.127
May 22	.99	3.61	2.94	4.60	22.84	.124	.150
	1.64	5.33	2.33	6.97	40.84	.133	.117
May 27	1.49	5.04	3.90	6.53	32.47	.226	.145
	2.40	8.81	2.24	11.21		.138	.128
June 1	1.05	3.61	3.67	4.66	24.07	.231	.142
	1.81	9.82	2.79	11.63	75.32	.070	.124
June 7	1.53	9.04	2.97	10.57	52.53	.170	.144
	2.48	13.96	2.46	16.44	83.53	.124	.134

EFFECT OF SODIUM CHLORATE ON ROOT RESERVES

The use of sodium chlorate in the control of noxious weeds is a common and successful practice. Recommendations vary, especially regarding the rate of application. Most workers agree that the best results are obtained when the chemical is applied in late summer or early fall.

Experiments were designed to study the root reserves of whiteweed as affected by a combined treatment of sodium chlorate and cultivation. Two series of plots which were uniformly infested with whiteweed were selected. One group of plots was cultivated three times,

May 1, May 12, and May 20, 1936; the other was left undisturbed. On June 1, and at irregular intervals thereafter (tables 6 and 7), root samples were taken from one plot each of the undisturbed and cultivated plants, and immediately thereafter dry sodium chlorate was applied to each sampled plot at the rate of 3 pounds per square rod. One month later root samples were again collected from the chlorate-treated plots and two new plots (one cultivated and one undisturbed) were sampled and treated with sodium chlorate as stated. The same system was followed throughout the season except in September, when samples were taken and treatments were made at 2-week intervals.

The experiment was repeated in 1937. The plots were cultivated May 8 and May 17, and sodium chlorate was first applied June 7, when the first root samples were taken. The data are given in tables 6 and 7. In both experiments a light irrigation, which served to carry the sodium chlorate into the soil, was made at regular intervals.

TABLE 6.—*Effect of combined treatment with sodium chlorate and cultivation on the carbohydrate content (percent) of whiteweed roots, 1936*

[The two sets of data for each sampling date are for the first- and second-foot levels, respectively]

SAMPLED AT TIME OF TREATMENT

Date of sampling	Undisturbed plants					Cultivated plants				
	Total sugars	Starch	Acid-hydrolyzable substances	Readily available carbohydrates on the basis of—		Total sugars	Starch	Acid-hydrolyzable substances	Readily available carbohydrates on the basis of—	
				Fresh weight	Dry weight				Fresh weight	Dry weight
June 1	2.24	9.67	5.15	11.91	47.83	1.61	1.94	2.82	3.55	31.42
	2.80	9.43	3.16	12.23	66.05	2.65	2.64	2.27	5.29	55.00
June 30	2.38	9.98	4.44	12.36	44.39	1.98	3.93	3.37	5.91	40.08
Aug. 2	2.77	21.24	4.74	24.01	68.57	1.95	13.65	4.59	15.60	54.54
	2.88	22.43	4.33	25.31	71.70	2.17	22.17	3.20	24.34	89.67
Sept. 1	1.98	17.04	4.86	19.02	54.81					
	2.96	20.19	3.18	23.15	76.55					
Sept. 17	2.16	15.38	5.05	17.54	55.15					
	2.24	21.27	3.13	23.51	79.93					
Sept. 30	2.51	14.77	4.86	17.28	64.14					
	2.04	21.14	3.09	23.18	82.78					

SAMPLED 1 MONTH AFTER TREATMENT

June 30	1.50	9.61	5.25	11.11	48.05	1.27	2.89	2.95	4.16	34.26
Aug. 1	2.22	11.28	4.61	13.50	49.55	1.66	6.19	3.25	7.85	48.30
	2.83	12.42	3.48	15.25	66.26	1.92	5.95	2.57	7.87	57.09
Sept. 1	2.07	14.32		16.39	49.30	2.13	11.55	3.90	13.68	53.85
	2.53	21.05	3.68	23.58	77.05	1.91	10.71	2.01	12.62	65.11
Sept. 30	2.34	13.20	4.83	15.54	57.98					
	2.12	20.87	3.46	22.99	85.11					
Oct. 16	2.98	11.38	3.23	14.36	52.79					
	2.77	15.55	3.64	18.32	70.46					
Oct. 29	5.20	12.83	4.99	18.03	68.04					
	4.16	18.80	3.58	22.96	88.65					

TABLE 7.—*Effect of combined treatment with sodium chlorate and cultivation on the carbohydrate content (percent) of whiteweed roots, 1937*

[The two sets of data for each sampling date are for the first- and second-foot levels, respectively]

SAMPLED AT TIME OF TREATMENT

Date of sampling	Undisturbed plants					Cultivated plants				
	Total sugars	Starch	Acid-hydrolyzable substances	Readily available carbohydrates on the basis of—		Total sugars	Starch	Acid-hydrolyzable substances	Readily available carbohydrates on the basis of—	
				Fresh weight	Dry weight				Fresh weight	Dry weight
June 7						1.53	9.04	2.97	10.57	52.53
						2.48	13.96	2.46	16.44	83.53
July 6	2.13	16.08	2.62	18.21	50.63	2.05	8.70	1.89	10.75	41.02
	3.07	22.33	1.90	25.40	71.10	2.34	5.36	1.66	7.67	39.56
Sept. 13	1.81	18.69	5.27	20.50	68.19					
	2.22	16.95	11.68	19.17	62.01					

SAMPLED 1 MONTH AFTER TREATMENT

July 6						3.27	2.75	3.60	6.02	30.08
						1.68	3.65	1.41	5.33	33.58
Aug. 9	1.14	17.90	2.65	19.04	54.58	.81	9.00	4.62	9.81	38.85
	1.57	21.10	5.79	22.67	62.72	1.10	8.97	3.34	10.07	53.60
Oct. 12	2.56	10.99	1.03	13.55	45.77					
	2.91	15.93	2.87	18.84	65.96					

Although the data would have been more complete had samples been taken from all previously sampled plots at each sampling date,

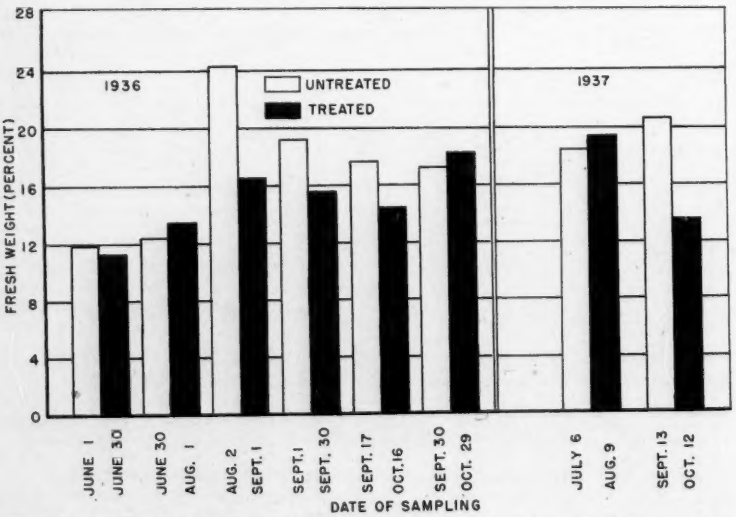

FIGURE 7.—Carbohydrate content of whiteweed roots as affected by date of application of sodium chlorate to undisturbed plots.

some interesting information is revealed by the results. The undisturbed plants showed the expected accumulation of carbohydrates.

Application of sodium chlorate to undisturbed plants had only a moderate effect in reducing the carbohydrate content in a period of 1 month after treatment regardless of the date.

A study of tables 6 and 7 and a comparison of figures 7 and 8 show that an early-season cultivation did not increase the effectiveness of the sodium chlorate applied immediately after the cultivation, which is in accord with results previously obtained with bindweed under Colorado conditions (*4*). On the basis of results obtained in this experiment, therefore, it is concluded that no greater reduction of the carbohydrates in the roots of whiteweed could be expected by the

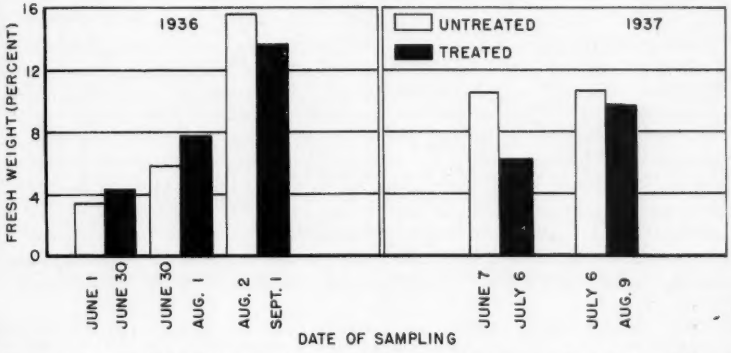

FIGURE 8.—Carbohydrate content of whiteweed roots as affected by date of application of sodium chlorate to cultivated plants.

application of sodium chlorate to cultivated plants than to undisturbed plants.

EFFECT OF FREQUENCY OF CULTIVATION ON ROOT RESERVES

The carbohydrate content of undisturbed whiteweed roots is compared in table 8 with that of plants cultivated at weekly and biweekly intervals during one season. The samples were collected September 30, 1936. Regrowth of plants on all the cultivated plots was extremely limited by the middle of July. Biweekly cultivations seemed to control the plant as well as the weekly cultivations.

The data of table 8 show very clearly the relative condition of the cultivated and undisturbed plants at the end of the growing season.

TABLE 8.—*Effect of frequency of cultivation on root reserves in whiteweed*

[Sampled September 30, 1936]

Treatment	Sugar	Starch	Acid-hydrolyzable substances	Readily available carbohydrates on basis of—	
				Fresh weight	Dry weight
	Percent	*Percent*	*Percent*	*Percent*	*Percent*
Undisturbed	2.51	14.77	4.86	17.28	64.17
Cultivated biweekly	2.41	3.43	1.56	5.84	62.14
Cultivated weekly	2.02	3.84	1.99	5.86	52.14

In these experiments cultivation was 96 to 98 percent effective in controlling whiteweed. The readily available reserve food in the remaining 4 to 2 percent of the plants amounted to about 5.85 percent. That moderately high value probably is misleading, however, a fact that becomes apparent only when it is considered that the samples upon which the analyses were made were collected from many scattered plants surving on the cultivated plots. All other samples were from areas chosen at random.

SUMMARY

The root reserves in whiteweed, *Cardaria draba* var. *repens*, have been studied. Data have been presented to show the seasonal trend of carbohydrates in both noncultivated and cultivated plots. Samples collected at 2-week intervals from April 25 to October 29 from noncultivated plots showed a maximum accumulation of carbohydrates about August 1. The lowest carbohydrate content was found early in the season when sampling was started. The total sugar content was higher in the roots from the second foot of soil than in those from the first-foot level until about the middle of September. The root reserves were present chiefly in the form of starch. The starch content of undisturbed plants reached a maximum of over 21 percent fresh weight but the total sugar content never exceeded 7.44 percent and reducing sugars remained uniformly low, reaching a maximum of 1.41 percent.

Clean cultivation held the starch content to about 4.50 percent and total sugars to less than 3.50 percent.

Both soluble and colloidal nitrogen decreased during the vegetative growth of the plants and showed a slight but apparent increase after flowering.

Samples collected at 4-day intervals for a period of 24 days after a single cultivation showed no material change in carbohydrate reserves until about 14 to 16 days after cultivation. After that there was an appreciable accumulation of carbohydrates.

Treatment with sodium chlorate accompanied by an early season cultivation did not increase the effectiveness of the chemical treatment in the control of whiteweed.

Biweekly cultivations were equally as effective as weekly cultivations in reducing the root reserves and in controlling the weed.

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